
OSTEOLOGY AND PHYLOGENY OF THE CUTLASSFISHES (SCOMBROIDEI: TRICHIURIDAE)

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ABSTRACT. This study describes the osteology and otolith morphology of the genera of the Trichiuridae. Evolutionary relationships of the group are investigated based on a cladistic analysis of adult characters. Evidence is provided for the monophyly of the trichiurids. The data support the following phyletic sequence among the genera and clades: *Aphanopus*, *Benthodesmus*, *Lepidopus caudatus*-*L. fitchi* clade, *Lepidopus altifrons*-*Evoxymetopon* clade, *Assurger*, *Tentoriceps*, *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*. Osteological data suggest that *Lepidopus* is paraphyletic. In addition, the sister group relationship of a gempylid clade *Diplospinus*-*Paradiplospinus* to the trichiurids is strongly supported. The most parsimonious hypotheses of relationships indicate that the caudal fin has been lost only once during the evolution of the trichiurids, whereas the pelvic fin appears to have disappeared or become reduced twice within the group and independently in the outgroup *Paradiplospinus*. The data of this study are compared with previous studies on trichiurid morphology and analyses of relationships among the scombroids. Prior studies, particularly those based on analysis of ontogenetic characters, support the results of the study reported herein.

INTRODUCTION

The trichiurids, commonly known as cutlassfishes, hairtails, frostfishes, scabbardfishes, or ribbonfishes, are benthopelagic predators inhabiting the con-

tinental shelf and slope worldwide. Their habitats in tropical and temperate regions range from estuaries to open water 2,000 m in depth. Adults are generally identified by their extremely elongate, laterally compressed bodies; a cluster of long, fang-like teeth on the premaxillary symphysis; presence of a single nostril on each side of the head; a lachrymal that covers most of the descending arms of the maxilla and premaxilla; and reduction or ab-

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sence of the caudal and pelvic fins in some genera. Although not as important commercially as their tuna and billfish relatives, some species of cutlassfishes constitute valuable fisheries in several areas of the world, such as the East China Sea, the North Indian Ocean, and the Mediterranean (Ye and Rosenberg, 1991; Nakamura and Parin, 1993).

Most authors separate the cutlassfishes and the closely related snake mackerels into the Trichiuridae and Gempylidae, respectively. Nakamura and Parin (1993) included the Gempylidae and Trichiuridae within the superfamily Trichiuroidea, suborder Scombroidei.

The Trichiuridae comprises at least 35 species belonging to the following nine genera: *Aphanopus* Lowe 1839, *Assurger* Whitley 1933, *Benthodesmus* Goode and Bean 1882, *Eupleurogrammus* Gill 1862, *Evoxymetopon* Gill 1863, *Lepidopus* Goüan 1770, *Lepturacanthus* Fowler 1905, *Tentoriceps* Whitley 1948, and *Trichiurus* Linnaeus 1758 (Nakamura and Parin, 1993; Parin, 1995). Evidence for the monophyly of the trichiurids has been presented previously (Collette et al., 1984; Johnson, 1986), and most authors have concluded that these fishes represent a highly derived branch of some group of gempylids (Tucker, 1956; Matsubara and Iwai, 1958; Parin and Becker, 1972; Collette and Russo, 1986; Johnson, 1986; Potthoff et al., 1986; Nakamura and Parin, 1993; Carpenter et al., 1995). In a cladistic classification of the scombroids, Johnson (1986) placed the cutlassfishes (his subfamily Trichiurinae) and the snake mackerels (his subfamilies Gempylinae and Lepidocybiinae) as part of his Gempylidae. Throughout this manuscript, the most common usage of the names Trichiuridae and Gempylidae (their limits according to the classification presented by Nakamura and Parin, 1993) is maintained to avoid confusion when reviewing the literature. Thus, unless otherwise indicated, Trichiuridae (cutlassfishes) and Gempylidae (snake mackerels) refer to the Trichiurinae and Gempylinae plus Lepidocybiinae of Johnson (1986), respectively.

In this study, a cladistic hypothesis of relationships among the genera of the Trichiuridae (*sensu* Nakamura and Parin, 1993) is proposed, using a comparative analysis of adult osteology, including otoliths. The hypothesis constructed with adult characters is compared to previous hypotheses of relationships and, in particular, with that of Gago (1997), which was based on larval characters.

HISTORICAL BACKGROUND

The trichiurids and gempylids were recognized as scombroids by Cuvier (in Cuvier and Valenciennes, 1832). Later workers proposed variations on classifications of the trichiurids and considered the gempylids and trichiurids to be closely related (Swainson, 1839; Günther, 1860; Gill, 1863; Capello, 1868; Goode and Bean, 1895; Boulenger, 1904; Goodrich, 1909).

Since the definition of the Scombroidei proposed

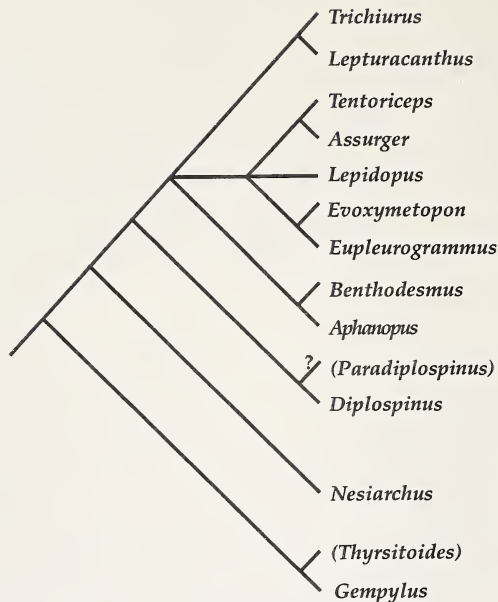


Figure 1. General diagram of the hypothesis of relationships between the trichiurid genera according to Tucker (1956). In parentheses: *Mimasea* (= *Thyrsitoides*) was included in Tucker's (1956) study but is not part of this analysis; *Paradiplospinus* was not recognized at the time of Tucker's (1956) study, but it is included in this analysis.

by Regan (1909), the trichiurids have consistently been included in this suborder. Regan (1909) considered the Scombroidei to comprise the Gempylidae, Istiophoridae, Luvaridae, Scombridae, Trichiuridae, and Xiphiidae. The trichiurids and gempylids were placed within his division Trichiuriformes, characterized by: caudal fin rays not deeply forked at the base; premaxilla beak-like and detached from the nasals; mouth with a lateral cleft and strong anterior canines; epiotic separated by the supraoccipital; gill membranes free from the isthmus; and pectoral fins located low on the body.

Starks (1911) and Gregory (1933) suggested a close relationship between *Gempylus* Cuvier 1829 and the trichiurids. Matsubara and Iwai (1958) suggested that the gempylids *Gempylus* and *Mimasea* (= *Thyrsitoides*) Fowler 1929 are the most closely related genera to the trichiurids and that *Gempylus* approaches the "primitive trichiurid" *Diplospinus* Maul 1948 in several characters.

Tucker (1956) presented the first modern comparative study of the trichiurids, including a more thorough analysis of the gempylid-trichiurid relationships. Figure 1 shows a general diagram of the hypothesis of Tucker (1956) based on his figure 26. He divided the Trichiuridae into three subfamilies: Aphanopodinae (Gill, 1863), including *Aphanopus*, *Benthodesmus*, and *Diplospinus*; Lepidopodinae (Gill, 1863), including *Assurger*, *Eupleurogrammus*, *Evoxymetopon*, *Lepidopus*, and *Tentoriceps*;

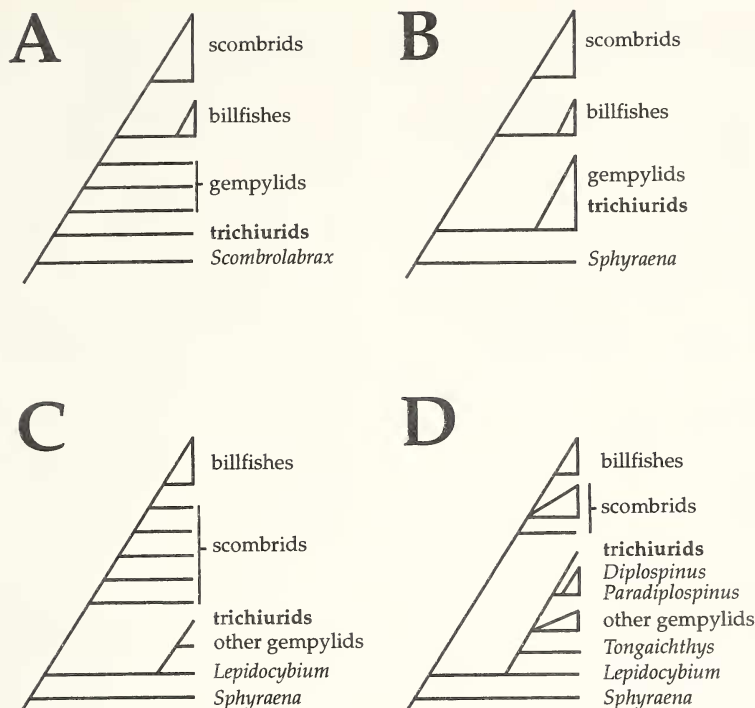


Figure 2. General diagrams of the hypotheses of relationships among the scombroids based on morphological data and following the work of: (A) Collette et al. (1984); (B) Collette and Russo (1986); (C) Johnson (1986); (D) strict consensus tree from figures 5–8 of Carpenter et al. (1995).

Trichiurinae (Swainson, 1839), including *Lepturacanthus* and *Trichiurus*. Tucker (1956) also considered the trichiurids as an offshoot of the gempylids, and he suggested that the gempylids *Gempylus*, *Nesiarchus* Johnson 1862, and *Mimasea* (= *Thyrstitoides*) are the most closely related to the trichiurids. He hypothesized that *Diplospinus* and *Nesiarchus* represent the bridge connecting the two families, and he considered *Diplospinus* as the most primitive trichiurid. However, Tucker (1956: 125) noted that “whether the Trichiurinae crossed the same bridge or by a parallel bridge further downstream is still debatable.” Andriashev (1960) described *Paradiplaspinus antarcticus* and considered it the most primitive representative of the Aphanopodinae of Tucker (1956). Parin and Becker (1970) recognized the Aphanopodinae of Tucker (1956) as a natural group excluding *Diplospinus* and *Paradiplaspinus*. Parin and Becker (1972) removed *Diplospinus* and *Paradiplaspinus* from the Trichiuridae and included them with the gempylids based on the following characters: two external nares on each side; the number of dorsal-fin pterygiophores does not correspond to the number of neural spines; a low number of caudal vertebrae; and a gempylid-like larval morphology. They placed *Diplospinus* and *Paradiplaspinus* in the Gempylidae but noted that these two genera occupy an intermediate position between the gempylids

and the trichiurids. Furthermore, they indicated that *Aphanopus* is the most primitive genus within the trichiurids.

Collette et al. (1984) placed the trichiurids as the sister group of all other scombroids, except *Scombrabrax heterolepis* Roule 1921, which they used to root their cladogram (Fig. 2A). In their hypothesis of relationships the gempylids appeared as a paraphyletic group. Collette and Russo (1986) re-evaluated the previous phylogeny and presented a hypothesis of relationships in which the trichiurids appeared to form a monophyletic group with the gempylids *Gempylus*, *Nealotus* Johnson 1865, *Nesiarchus*, *Promethichthys* Gill 1893, *Rexea* Waite 1911, *Thyrstitoides*, and *Tongaichthys* Nakamura and Fujii 1983 (Fig. 2B).

Johnson (1986) discussed the cladistic analysis of Collette et al. (1984) and proposed an alternative hypothesis of scombroid relationships (Fig. 2C). He defined the monophyly of the trichiurids based on nine meristic, osteological, external anatomy, and larval morphology synapomorphies, including two reversals. He recognized three gempylid subfamilies: Lepidocybiinae [including only *Lepidocybium flavobrunneum* (Smith 1849)]; Gempylinae [Gempylidae of Collette et al. (1984), excluding *L. flavobrunneum*]; and Trichiurinae [Trichiuridae of Collette et al. (1984)]. In Johnson’s (1986) hypothesis, *Scombrabrax* Roule 1921 was placed as an

outgroup and *Sphyræna* Röse 1793 was included within the Scombroidei as the sister group to all other scombroids. Johnson (1986) considered his Gempylidae as the sister group of all other scombroids, except *Sphyræna*. He also placed *Lepidocybium* Gill 1862 as the sister group of all the other gempylids and trichiurids. He concluded that his monophyletic Trichiurinae represented a highly specialized branch of the Gempylidae with some small group of his subfamily Gempylinae being its sister group. Johnson (1986) noted the need for more systematic work to resolve the precise relationships among gempylids and trichiurids.

Potthoff et al. (1986) described the development of bone and cartilage in several scombroid groups. They noted that the gempylids and the trichiurids are very closely related and that the trichiurids represent a group derived from the gempylids.

The work of Block (1991), Block et al. (1993), and Finnerty and Block (1995; Fig. 3) and data presented by Finnerty and Block at the 1994 meetings of the American Society of Ichthyologists and Herpetologists addressed the question of scombroid phylogeny using molecular systematics. Although all of their molecular data sets have consistently supported the monophyly of the billfishes and their separation from the gempylids, scombrids, and trichiurids, the placement of *Trichiurus lepturus* Linnaeus 1758 and *Gempylus serpens* Cuvier 1829 (the only trichiurid and gempylid used in their analysis) is very unstable.

Carpenter et al. (1995) examined different hypotheses of scombroid relationships obtained by re-analyzing the data of Johnson (1986), analyzing the revised combined data sets of Collette et al. (1984) and Johnson (1986), and reinterpreting the gill raker character of Johnson (1986: character 44). A summary diagram of Carpenter et al.'s (1995) hypothesis is shown in Figure 2D. The different analyses based on the revision of Johnson's (1986) data set did not change his original hypothesis of relationships among the gempylids and the trichiurids. In these revised analyses the trichiurids always appeared as an offshoot of some group of the gempylids (gempylines of Johnson, 1986), and *Lepidocybium* appeared as the sister group of all the other gempylids and trichiurids. All of the resulting cladograms from the analysis of Carpenter et al.'s (1995) expanded data matrix, which included the data of Collette et al. (1984) and Johnson (1986), also agreed with the hypothesis of relationships among the gempylids and trichiurids proposed by Johnson (1986). The expanded analyses of Carpenter et al. (1995), including their change in the coding of Johnson's (1986) character 44, always resulted in placing *Diplospinus* (which includes *Paradiplospinus* in their data matrix) as the sister group of the trichiurids. The relationships among the rest of the gempylids, except *Lepidocybium* and *Tongaichthys*, which always appear in that phyletic order as the sister groups of the gempylids and trichiurids, were unresolved in the unweighted anal-

ysis of Carpenter et al.'s (1995) expanded data matrix (their figs. 5, 7). The placement of *Gempylus* and *Nesiarchus* (two genera that have been previously proposed as being closely related to the trichiurids) in Carpenter et al.'s (1995) weighted analyses was variable. A strict consensus tree of their 142 most parsimonious trees obtained after successive character weighting of their expanded data matrix (their fig. 6) placed *Nesiarchus* as the sister group to an unresolved clade including the gempylids *Epinnula* Poey 1854, *Ruvettus* Cocco 1829, and *Thyrsitoides*. *Gempylus* appeared as part of a trichotomy that includes *Nealotus* Johnson 1865 and a clade including *Epinnula*, *Nesiarchus*, *Promethichthys*, *Ruvettus*, *Thyrsitoides*, and *Thyrsitops* Gill 1862. In their weighted analysis based on a different interpretation of a gill raker character (their fig. 8), *Nesiarchus* appeared as the sister group of a clade that includes *Epinnula*, *Neoepinnula* Matsubara and Iwai 1952, *Ruvettus*, and *Thyrsitoides*. *Gempylus* appeared as part of a trichotomy with *Nealotus* and a clade that includes all of the six taxa above plus *Promethichthys* and *Thyrsitops*. Carpenter et al. (1995) concluded that a data set with more characters that vary within the gempylids and trichiurids would be necessary to resolve the relationships among these groups.

Gago (1997) analyzed the relationships among the trichiurids based on a data matrix of ontogenetic characters. He included most gempylids as the outgroups and rooted the resulting trees at *Lepidocybium*. The results of his analysis did not resolve the relationships among the gempylids. However, the ontogenetic data increased the support for the monophyly of the trichiurids. Within the trichiurids, he found that those genera lacking a well-developed caudal fin complex constitute a clade.

MATERIALS AND METHODS

Comparative Material

The comparative material is listed in alphabetical order according to the taxon and the institutions that provided the specimens. The catalogue number is followed by the number of specimens and the range (within parentheses and in mm) of standard lengths (SL; when a caudal fin is present) and total lengths (TL; taxa without a caudal fin). A question mark indicates unknown or unavailable data. All specimens listed are cleared and stained, except those followed by the abbreviation "sk," which indicates skeletonized material. Many radiographs and alcohol-preserved specimens as well as cleared and stained specimens from uncatalogued collections were also studied, but are not listed here. Institutional abbreviations follow Leviton et al. (1985). Species names are those recognized by Nakamura and Parin (1993) and Parin (1995).

Gempylidae

Diplospinus multistriatus Maul 1948: LACM 45450-1 (1; 193 SL), 45604-2 (2; 178, ≈183 SL); USNM 194475 (1; ≈172 SL).

Gempylus serpens: LACM 34160-8 (1; 430 SL).

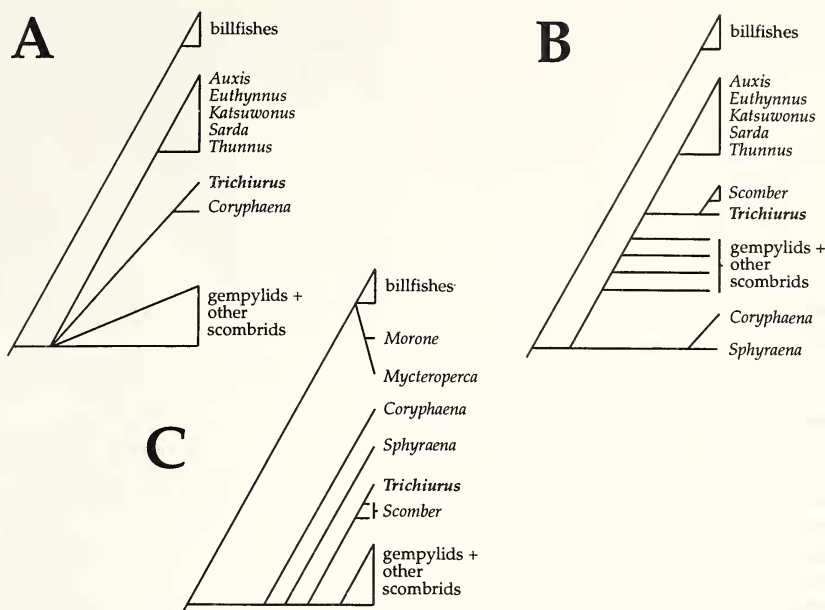


Figure 3. General diagrams of the hypotheses of relationships among the scombroids based on the cytochrome *b* gene data of Finnerty and Block (1995: figs. 2, 4, 7): (A) unweighted analysis of nucleotide substitution data; (B) weighted analysis of nucleotide substitution data; (C) amino acid sequence data.

Nesiarchus nasutus Johnson 1862: USNM 236803 (1; 67 SL), 324038 (1; 276 SL).
Paradiplospinus antarcticus Andriashev 1960: LACM 10942 (1; 283 SL), 11325-22 (1; 198 SL), 11511 (1; 278 SL); USNM 208448 (1; 320 SL).

Trichiuridae

Aphanopus arigato Parin 1995: LACM 37113-1 (1; 968 SL), 38240-1 (1; 648 SL).
Aphanopus carbo Lowe 1839: AMS I.25852004 (1; 418 SL).
Assurger anzac (Alexander 1916): SIO 63-229 (1; ≈750 SL).
Benthodesmus simonyi (Steindachner 1891): USNM 292768 (1; 537 SL).
Benthodesmus tenuis (Günther 1877): LACM TC61-117 (1; 522 SL); SIO 82-43 (1; 369 SL).
Eupleurogrammus glossodon (Bleeker 1860): LACM 38131-15 (1; 356 TL), 38134-14 (1; 345 TL).
Evoxymetopon taeniatum Gill 1863: USNM 321690 (1; 190 SL).
Lepidopus altifrons Parin and Collette 1993: USNM 292765 (1; ≈390 SL), 317979 (1; ≈345 SL).
Lepidopus caudatus (Euphrasen 1788): AMS IA.7041 as *L. lex* (1; ?)sk; USNM 268911 (1; ≈246 SL).
Lepidopus fitchi Rosenblatt and Wilson 1987: LACM 31683-1 (1; ≈239 SL), 32684-1 (1; 185 SL), 37102-1 (1; 685 SL)sk, 37102-2 (1; 785 SL)sk, 37103-1 (1; ≈900 SL)sk, 38511-1 (1; 272 SL), 45602-1 (3; 198-223 SL), 45855-1 (1; 275 SL); SIO 72-84 (2; 152-164 SL), 72-209 (1; 237 SL).
Lepturacanthus savala (Cuvier 1829): AMS IB. 1797 (1; ?)sk; LACM 38131-16 (1; 421 TL), 38134-15 (1; >275 TL), 38136-21 (1; 376 TL).
Tentoriceps cristatus (Klunzinger 1884): AMS I.17805002

as *Tentoriceps* sp. nov. (1; 301 TL), I.22830008 (1; 354 TL); LACM 44793-11 (1; 310 TL).

Trichiurus lepturus: AMS IB.7447 as *T. coxii* Ramsay and Ogilby 1887 (1; ?)sk; LACM 6945-11 (1; 340 TL), 37104-1 as *T. nitens* Garman 1899 (1; 488 TL)sk, 37906-22 (1; 452 TL)sk, 37955-1 (1; ?)sk, 37955-2 (1; ?)sk, 37955-3 (1; ?)sk, 37956-1 (1; ?)sk, 37957-1 as *Trichiurus* sp. (1; ?)sk, 38117-100 as *T. nitens* (1; 1060 TL)sk, 38117-101 (1; 953 TL)sk, 33807-12 as *Trichiurus* sp. (1; 586 TL)sk, 38130-19 (1; 288 TL); SIO 55-58 (1; 281 TL).

I analyzed 336 sagittae from the Fitch otolith collection at the Natural History Museum of Los Angeles County. They included specimens of the following scombroid genera: *Aphanopus*, *Assurger*, *Benthodesmus*, *Lepidopus*, and *Trichiurus* (Trichiuridae); *Diplospinus*, *Gempylus*, *Lepidocybium*, *Nealotus*, *Paradiplospinus*, *Promethichthys*, *Rexea*, and *Ruvettus* (Gempylidae); *Euthynnus* Lütken 1882 (in Jordan and Gilbert 1882), *Grammatocercus* Gill 1862, *Scomberomorus* Lacepède 1801, and *Thunnus* South 1845 (Scombridae); *Istiophorus* Lacepède 1801, *Makaira* Lacepède 1802, and *Tetrapturus* Rafinesque 1810 (Istiophoridae); *Xiphias* Linnaeus 1758 (Xiphiidae). Six sagittae of the trichiurid species *Lepturacanthus savala* were obtained as a loan from the Australian Museum (I.21955-013). In addition, a drawing of the medial face of a left sagitta of the gempylid *Nesiarchus nasutus* (provided by D. Nolf, Institut Royal des Sciences Naturelles, Belgium), plus several descriptions and drawings of sagittae of other scombroid species (taken from the literature), were compared.

Comparative Analysis

Osteological characters were examined from radiographs, cleared and stained specimens, and dry skeletal prepara-

tions of adults. I followed the method of Porthoff (1984) for clearing and staining. A Wild M-5 dissecting microscope with a camera lucida was used for the preparation of drawings. Representative drawings of most of the adult osteological characters of each of the trichiurid genera are included for comparative purposes throughout the text. In most cases within the outgroups, I have only included osteological drawings of *Diplospinus* and *Paradiplospinus* since detailed drawings of most gempylids can be found in the work of Russo (1983). Osteological terminology follows mainly the works of Collette and Chao (1975) and Collette and Russo (1984), unless otherwise indicated.

The medial face of the sagittae was lightly rubbed with graphite for enhancement of morphological features. The sagittae were examined under a Wild M-5 dissecting microscope, and scanning electron microscopy was performed on representative specimens. Terminology for the otolith morphology follows Chaine and Duvergier (1934).

Phylogenetic Analysis

Polarity of the characters was determined by outgroup comparison. Choosing the outgroup is a critical step in cladistic analysis since character argumentation depends heavily on this decision. For the trichiurids this step was facilitated by the large amount of data available regarding scombroid interrelationships. As previously indicated, most workers have proposed a close relationship between gempylids and trichiurids.

Although noncladistic, the works of Tucker (1956) and Parin and Becker (1972) suggested that the gempylids *Diplospinus*, *Gempylus*, *Nesiarchus*, and *Paradiplospinus* are the best candidates for trichiurid outgroups. In addition, prior to the work of Parin and Becker (1972), *Diplospinus* and *Paradiplospinus* were included in the Trichiuridae. The consistent earlier placement of these two genera within the Trichiuridae was based on numerous similarities among these fishes and was interpreted by Tucker (1956) as evidence of common ancestry.

Johnson (1986) concluded that the trichiurids represent a highly derived offshoot of a paraphyletic Gempylidae (his subfamily Gempylinae). The work of Russo (1983) is particularly important because it provides a data matrix of osteological characters for the species of Gempylidae. Russo (1983) could not demonstrate the monophyly of the Gempylidae but concluded that the family comprises six groups. His most derived group was composed of the following genera in phyletic sequence: *Thyrstitoides*, *Nesiarchus*, *Gempylus*, and his *Paradiplospinus*-*Diplospinus* clade. Although *Paradiplospinus* was not recognized at the time of Tucker's (1956) study, *Diplospinus*, *Gempylus*, *Nesiarchus*, and *Mimasea* Kamohara 1936 (= *Thyrstitoides* Fowler 1929) were placed as the basal branches of his trichiurid tree. Furthermore, the results of the work of Carpenter et al. (1995) always placed the *Diplospinus*-*Paradiplospinus* clade as the sister group to the trichiurids.

A preliminary survey of the adult osteology and otolith morphology of the trichiurids and gempylids and its comparison with hypotheses and data sets presented by previous authors (Tucker, 1956; Parin and Becker, 1972; Russo, 1983; Collette et al., 1984; Johnson, 1986; Carpenter et al., 1995) indicate that *Diplospinus* and *Paradiplospinus* are the closest sister groups to the trichiurids. Thus, these two genera, plus *Gempylus* and *Nesiarchus*, are used as the outgroups in this study.

Trees were rooted at a basal polytomy with *Nesiarchus* and *Gempylus*, and following the conclusions of most authors, *Diplospinus* and *Paradiplospinus* were used as a clade representing the sister group to the trichiurids. For

those characters that appear to be heterogeneous among the outgroups and in which the hypothesized state at the outgroup node was equivocal (Maddison et al., 1984), the plesiomorphic condition was determined by comparison to the conditions in other gempylids and scombroids based on information taken from the literature. I agree with the conclusions of Russo (1983), Johnson (1986), and Carpenter et al. (1995) and consider *Lepidocybium* as the most basal gempylid. Thus, the plesiomorphic condition is assumed to be that present in *Lepidocybium*. If the condition in *Lepidocybium* is unknown, the plesiomorphic condition is assumed to be that which is most common among other gempylids or scombroids. Although "most common" does not necessarily indicate plesiomorphy (Maddison et al., 1984; Wiley et al., 1991), "the primitive state of a character for a particular group is likely to be present in many of the representatives of closely related groups" (Kluge and Farris, 1969 p. 5). Maddison et al. (1984) indicated that this form of outgroup methodology can lead to cladograms that are not globally parsimonious. This type of character assessment is used in this study, but more definite conclusions on the polarity of those characters that appear to be equivocal must await the results of a study in progress that includes all gempylids and trichiurids (F.J. Gago and J.L. Russo, unpublished data). The distribution among other gempylids and scombroids of the conditions of those characters that are equivocal is discussed under each of the osteological sections where these characters are described.

A data matrix of characters (Table 1) was constructed using MacClade version 3 (Maddison and Maddison, 1992) and analyzed with PAUP version 3.1.1 (Swofford, 1993). Character states were coded as numerals and "?," where 0 represents the plesiomorphic condition and "?" missing or nonapplicable data

RESULTS

All multistate characters (Table 1) were considered unordered, and the trees were rooted at a basal polytomy with *Gempylus* and *Nesiarchus*. An analysis using the branch-and-bound algorithm and ACCTRAN transformations resulted in three equally most parsimonious trees. These three trees have 99 steps, a consistency index of 0.869, and a rescaled consistency index of 0.809. All three trees have the same topology as the tree of Figure 4, except for the resolution between *Evoxymetopon*, *Lepidopus altifrons*, *L. caudatus*, and *L. fitchi*. Figure 5 shows the only portion of the topology among the most parsimonious trees that is variable. The variation in the topology of these trees is the result of different interpretations about the evolution of character 36. Figure 5 only includes character 36 since the interpretation of all the other characters analyzed using ACCTRAN is identical for all three trees at these variable nodes.

One tree places *Lepidopus caudatus* and *L. fitchi* as a monophyletic group (node IVa) and *Evoxymetopon* and *L. altifrons* as an unresolved polytomy at node V (Fig. 5A). In this tree the derived condition of character 36 is assumed to have evolved independently in the clade uniting *L. caudatus* and *L. fitchi* (node IVa) and in the monophyletic group above node V. This tree topology also

Table 1. Data Matrix of Adult Characters. 0 = plesiomorphic state; 1, 2, 3, 4 = apomorphic states; ? = missing data or not applicable.

Taxa	Characters					
	10	20	30	40	50	60
<i>Aphanopus</i>	100112000101000211010101001000000000100?01021020110000000212111110					
<i>Assurger</i>	110112011001000211011121111001111101100101021121211001000212111010					
<i>Benthodesmus</i>	120112001001000211010101001000110100100101021020210000000212111100					
<i>Eupleurogrammus</i>	1201120100110113210101110100012121111011121121311114121????????					
<i>Evoxymetopon</i>	120112011001000211011121111001111100100101021021311001000212111???					
<i>Lepidopus altifrons</i>	120112011001000211011121111001111100100101021021311001000212111???					
<i>L. caudatus</i>	120112011001000211010101101001111101100101021021311001000212111010					
<i>L. fitchi</i>	120112011001000211010101101001111101100101021021311001000212111010					
<i>Lepturacanthus</i>	12111211201111321010101101000121210111????21121311112121?????011					
<i>Tentoriceps</i>	12011201000100132101112111100112110111121121311113111?????????					
<i>Trichiurus</i>	12111211201111321010101101000121210111????21121311112121?????011					
<i>Diplospinus</i>	0000110000000002001000010001100000000001000100000000000102100100					
<i>Gempylus</i>	0000000001000001000000000000002002000100000000000000000000000000					
<i>Nesiarchus</i>	00					
<i>Paradiplospinus</i>	000011000000000200100001000110000000000?00010000000000000102100100					

assumes that character 36 reverted to the plesiomorphic condition at node IX.

A second tree places *Evoxymetopon* and *Lepidopus altifrons* as a clade (node Va) and *L. caudatus* and *L. fitchi* as an unresolved polytomy at node IV (Fig. 5B). Finally, the third tree places *L. caudatus* and *L. fitchi* and *Evoxymetopon* and *L. altifrons* in two separate clades, respectively (Fig. 5C, nodes IVa and Va). This last hypothesis of relationships has a “zero length” branch (node IVa), but it is included in the results of the analysis by PAUP to indicate that there is potential support for these monophyletic groups under some “most parsimonious reconstructions” (Swofford, 1993). The trees of Figure 5B and 5C assume that the derived condition of character 36 evolved only once below node IV and was lost independently in the clades including *Evoxymetopon* and *Lepidopus altifrons* (node Va) and *Lepturacanthus* and *Trichiurus* (node IX), respectively. A different interpretation of the third tree using DELTRAN assumes that the derived condition of character 36 evolved independently in the clade above node V and the clade of node IVa. This alternative hypothesis also concludes that character 36 reverted to the plesiomorphic condition in node IX and that the branch leading to node Va is “zero length.”

The tree in Figure 4 is not considered to be the final hypothesis of relationships. One must be aware that there are three equally parsimonious hypotheses as described earlier in this section and the tree of Figure 4 is just one of these hypotheses. However, because the three hypotheses differ only in the interpretation of a single character (character 36), the tree in Figure 4 serves as a good summary of the hypotheses of relationships and character evolution. The description that follows is based on the results of the analysis using ACCTRAN, as pre-

sented in Figure 4. An analysis of the tree in Figure 4 using DELTRAN results in different interpretations of character transformations for 10 of the characters utilized. For comparative purposes, Figure 6 shows the distribution of character states when using DELTRAN.

A monophyletic group including the gempylid genera *Diplospinus* and *Paradiplospinus* (node Ia) is supported by three synapomorphies and appears as the sister group of the trichiurids. The monophyletic group including these two outgroup genera plus the trichiurids (node I) is supported by 10 synapomorphies, including only one homoplasy.

Aphanopus appears as the sister group to the rest of the trichiurids at node II. A total of 21 synapomorphies, including only two homoplasies, support the monophyly of the trichiurids (node II).

The monophyly of the group that includes all the trichiurids except *Aphanopus* (node III) is supported by six synapomorphies, including three homoplasies. A monophyletic group including all trichiurids except *Aphanopus* and *Benthodesmus* (node IV) is supported by 10 synapomorphies, including four homoplasies.

As indicated earlier, in the tree of Figure 4 the branch leading to the monophyletic group of *Lepidopus caudatus* and *L. fitchi* is interpreted as having no support in the form of synapomorphies (zero length). However, the results using DELTRAN include character 36 as a synapomorphy at this node (Fig. 6).

The clade including *Evoxymetopon* and *Lepidopus altifrons* appears as the sister group to the monophyletic group that includes *Assurger*, *Tentoriceps*, *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*, in that phyletic order. The monophyletic group including these seven taxa (node V) is sup-

TL: 99
CI: 0.869
RC: 0.809

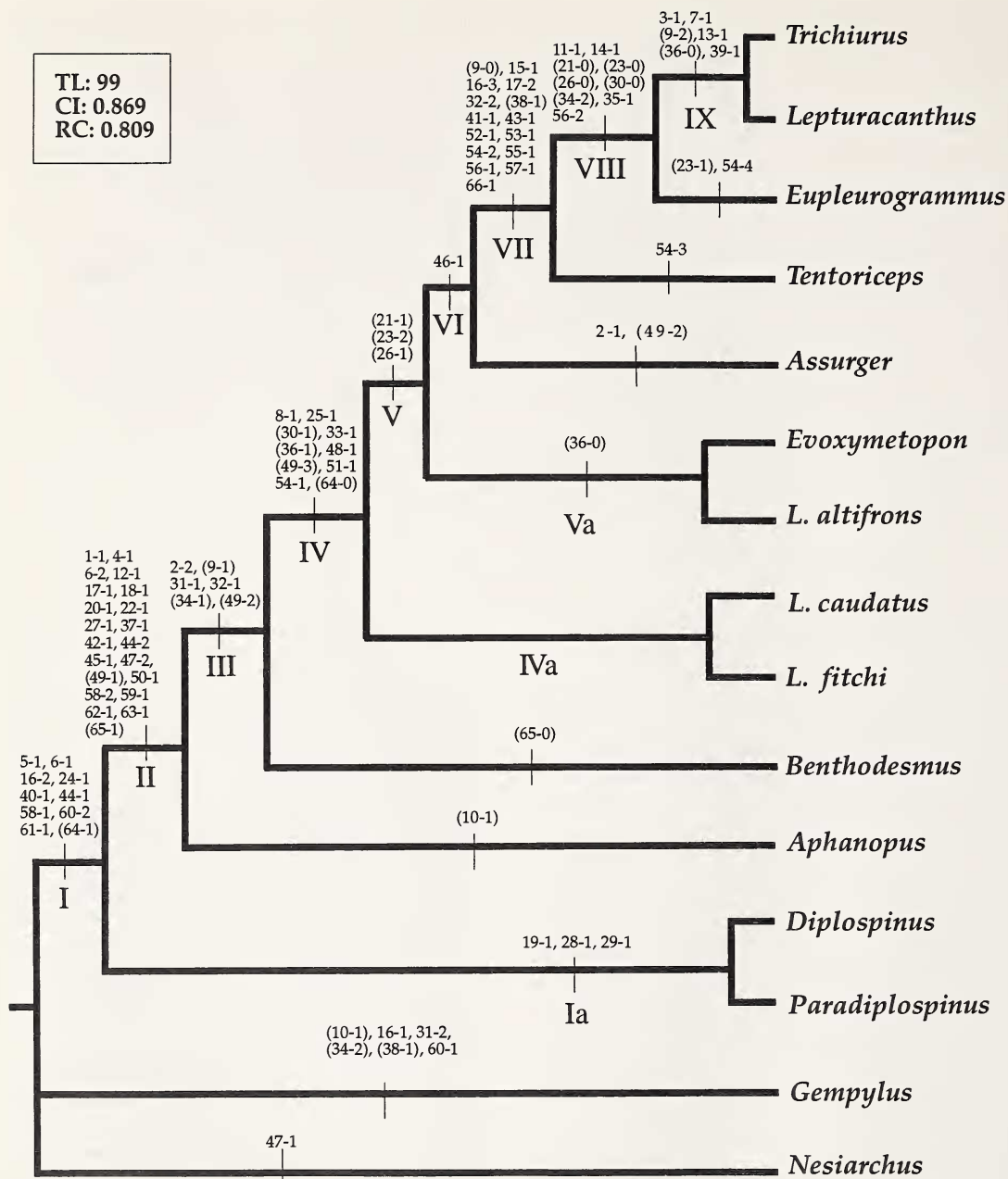


Figure 4. Hypothesis of relationships resulting from the branch-and-bound analysis of the data matrix. Character transformations follow ACCTRAN. Homoplastic characters are enclosed within parentheses; character numbers are followed by the state present at each respective node.

ported by three homoplasies (independent acquisitions).

A clade including *Evoxymetopon* and *Lepidopus altifrons* (node Va) is only supported by a reversal in character 36 (Fig. 5B, C). An analysis using DELTRAN includes this node, although it provides no support for its monophyly (Fig. 6; node Va).

Node VI places *Assurger* as the sister group to

the clade formed by *Tentoriceps*, *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*, but this is supported by only a single synapomorphy. The sister group relationship between *Tentoriceps* and the clade including *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* (node VII) is supported by 15 synapomorphies, including two homoplasies.

Furthermore, *Eupleurogrammus* appears as the

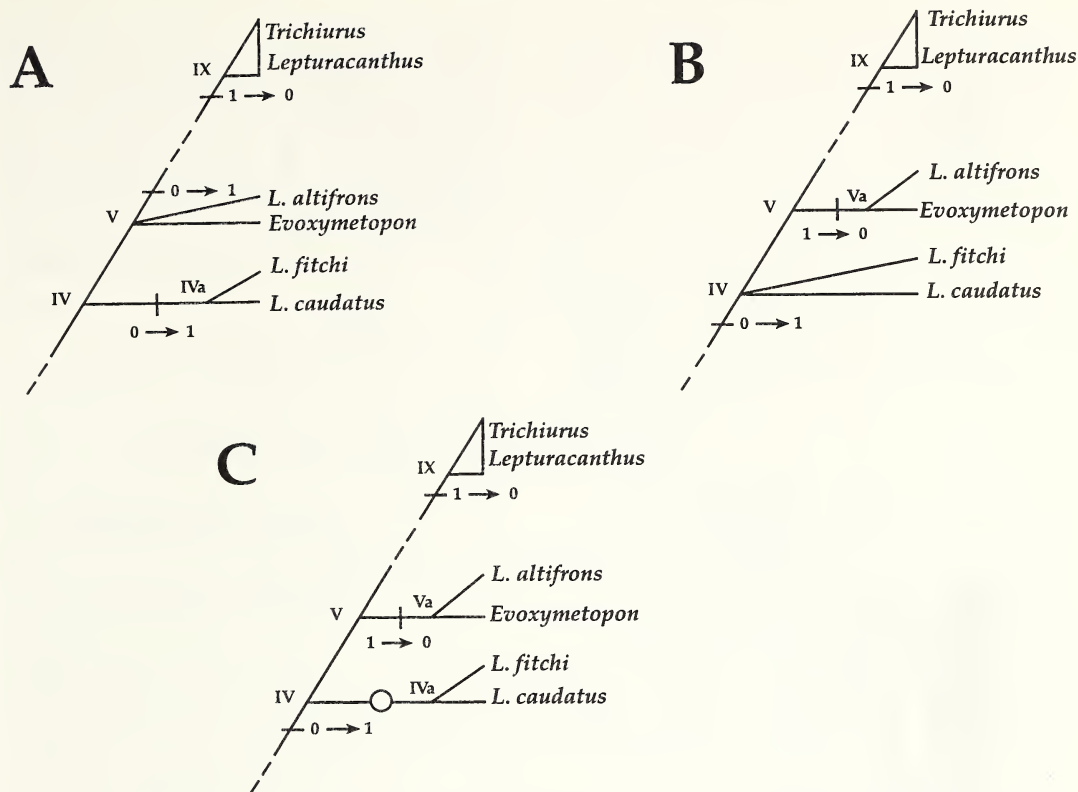


Figure 5. General diagrams of the most parsimonious hypotheses obtained during the branch-and-bound analysis of the adult data matrix (Appendix). Character transformations follow ACCTRAN. The direction of change between the states of character 36 (Appendix) is indicated with an arrow at each of the nodes. Dashed lines above and below nodes IV and V indicate portions of the hypotheses that are identical to those in the tree in Figure 4. Open circle = zero length branch.

sister group to *Lepturacanthus* and *Trichiurus* (node VIII). The monophyletic group including these three genera is supported by nine synapomorphies, including five homoplasies.

Lepturacanthus and *Trichiurus* appear as a monophyletic group (node IX). Six synapomorphies, including two homoplasies, support the monophyly of these two genera.

A tree with the topology presented by Tucker (1956; Fig. 1) was created using MacClade and imported into PAUP as a topological constraint for a branch-and-bound search using the data matrix of Table 1, but excluding *Paradiplospinus* and *Thyrsoitoides* from the analysis. As mentioned earlier, Tucker's (1956) tree places *Gempylus* (plus *Thyrsoitoides*, which was not included in this study), *Nesiarchus*, and *Diplospinus* (*Paradiplospinus* was not recognized at the time of Tucker's 1956 study), in that phyletic order, as the sister taxa of the trichiurids. He proposed three major groups in his tree: *Aphanopus-Benthodesmus* (his subfamily Aphanopodinae minus *Diplospinus*); *Lepturacanthus-Trichiurus* (his subfamily Trichiurinae); *Assurger-Eupleurogrammus-Evoxymetopon-Lepidopus-Tentoriceps* (his subfamily Lepidopodinae). The branches leading to these three groups appear as a trichotomy

above *Diplospinus*. Within his monophyletic Lepidopodinae he shows a trichotomy that included the following groups: *Assurger-Tentoriceps*; *Eupleurogrammus-Evoxymetopon*; *Lepidopus*. A branch-and-bound search with all characters treated as unordered resulted in three equally most parsimonious trees with a length of 134 steps and consistency and rescaled consistency indexes of 0.672 and 0.468, respectively. In all three resulting trees the clades *Aphanopus-Benthodesmus* and *Lepturacanthus-Trichiurus* appear, in that phyletic order, as the sister groups to Tucker's Lepidopodinae. The trees differ in the three possible resolutions among the clades proposed by Tucker (1956) within the Lepidopodinae.

DESCRIPTIVE OSTEOLOGY OF ADULTS

The characters for the phylogenetic analysis are indicated with numbers that correspond to those in the data matrix (Table 1), list of characters (Appendix), and phylogenies (Figs. 4–6). Character numbers are followed by the state present at each particular node. Character numbers in parentheses represent homoplasies.

TL: 99
CI: 0.869
RC: 0.809

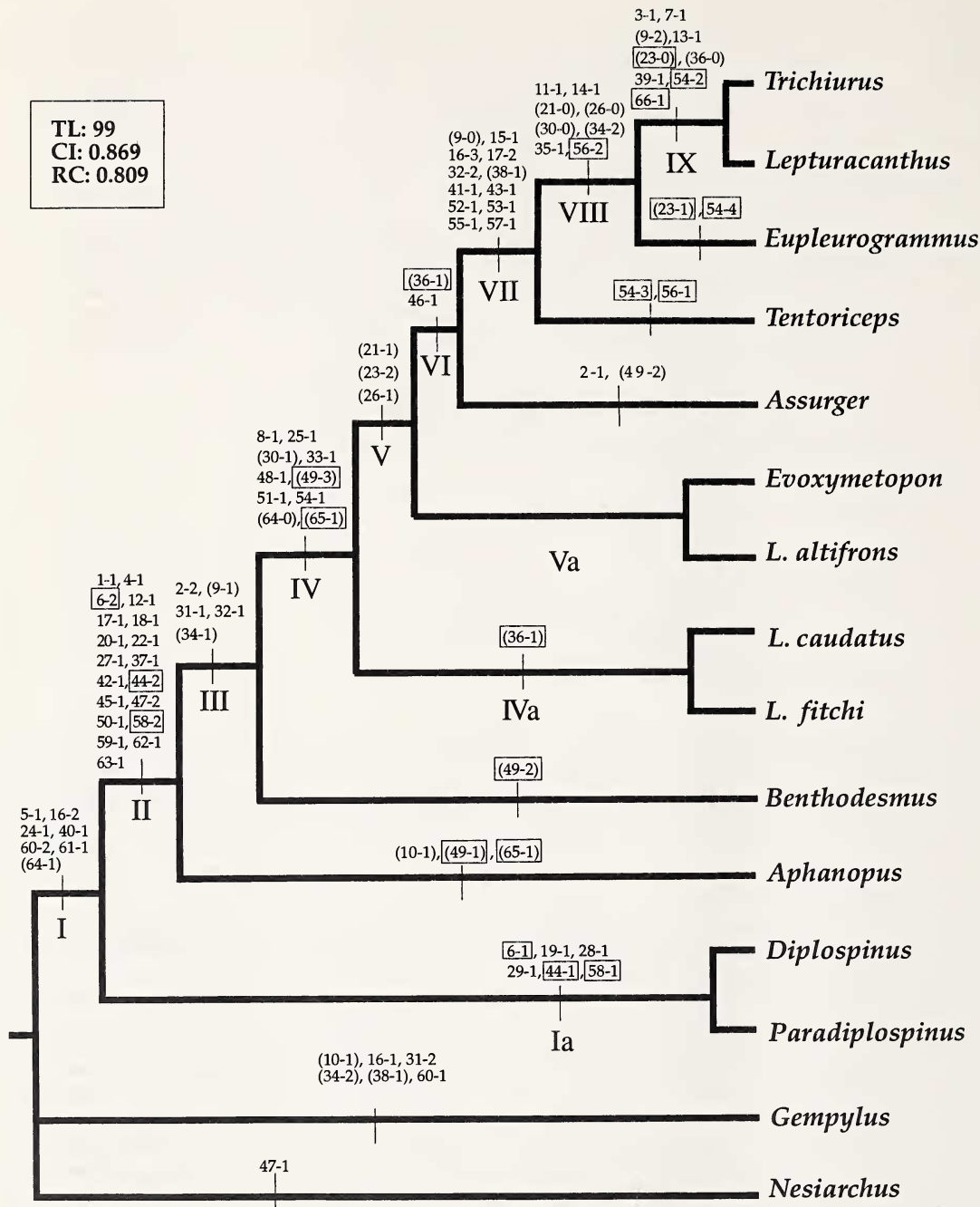


Figure 6. Hypothesis of relationships resulting from the branch-and-bound analysis of the data matrix. Character transformations follow DELTRAN. Homoplastic characters are enclosed within parentheses; character numbers are followed by the state present at each respective node. Those interpretations of character transformations that differ from the results using ACCTRAN (Fig. 4) are enclosed within a rectangle.

OPERCULAR SERIES

The bones of the opercular series in both the trichiurids and gempylids are poorly ossified. The thickest, most strongly ossified areas, which are the

articular corners of the opercle, subopercle, and interopercle, are spongy in appearance (Fig. 7).

Character 1. In the trichiurids, the posterior and ventral margins of the opercle, subopercle, and interopercle (the interopercle to a lesser degree) are

strongly splintered or fimbriated (Fig. 7C–K). Johnson (1986: character 26) considered this condition (including the ventral margins of the lachrymal) as a synapomorphy of his Trichiurinae. In the outgroups, the posterior and ventral margins of the opercle, subopercle, and interopercle are mostly complete (only the dorsal flap of the opercle and the posterior corner of the subopercle may be slightly splintered; Fig. 7A, B).

Opercle

The opercle of all gempylids and trichiurids is quadrilateral and characterized by the presence of a posterodorsal notch. Russo (1983: character 55) indicated that the posterodorsal notch in all gempylids, except *Gempylus* and *Lepidocybium*, is deep and bordered by a wide dorsal flap. In contrast, *Gempylus* and *Lepidocybium* have shallow opercular notches with a dorsal margin that tapers posteriorly to a point. The trichiurids have a deep dorsal notch and the dorsal flap above it is narrower than that in most gempylid genera, but it is not pointed.

Russo (1983: character 56) noted that all gempylids, except *Diplospinus*, *Gempylus*, *Lepidocybium*, *Nealotus*, *Nesiarchus*, *Rexea*, *Thyrsites* Cuvier (in Cuvier and Valenciennes 1832), and *Thyrstitoides*, bear a spinous ventral margin on the posterodorsal notch of the opercle. All of the trichiurids analyzed here have opercular notches with ventral margins that are not pointed or spinous. Some specimens of *Paradiplospinus* utilized in this study have a small feeble spinous ventral margin on the opercular notch, and one specimen of *Diplospinus multistriatus* has a spinous opercular notch on only one side of the body. The presence or absence of a spinous ventral margin on the opercular notch is variable within these two outgroup genera.

The opercle articulates with the posterior condyle of the hyomandibula by an anterodorsal articular head that houses an articular fossa. All gempylids, except *Lepidocybium*, and the trichiurids share this condition. At its base, the anterodorsal articular head bears one to three struts or ridges that support the main body of the opercle medially. The articular head is short in all the genera studied, except *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*, in which it clearly projects from the anterodorsal corner of the opercle by way of an elongate neck-like base. However, it is difficult to categorize this condition objectively because *Assurger*, *Evoxymetopon*, and *Lepidopus* share an intermediate state in the elongation of the articular head.

Character 2. The outgroup genera and the trichiurid *Aphanopus* have a lateral plate-like process at the anterodorsal corner of the opercle that covers all or most of the articular head (Fig. 8A). In all the other trichiurids, except *Assurger*, the articular head lacks a lateral plate, but it bears a well-developed elongate lateral process that is round in cross

section (Fig. 8C). *Assurger* also bears an elongate lateral process, but it is flat in cross section (Fig. 8B). In *Gempylus* the plate-like process is dorsally elongate, but the condition is not comparable with that of *Assurger*. The flat process of *Assurger* crosses the articular head of the opercle at about its center (as in those trichiurids with an elongate process that is round in cross section), whereas the flat process of *Gempylus* extends posterodorsally of the articular head and appears to be a modification of the plate covering the dorsal margin of the articular head. The lateral process is longer in *Assurger*, *Eupleurogrammus*, *Lepidopus*, *Tentoriceps*, and *Trichiurus*, but the degree of elongation is difficult to categorize objectively.

Subopercle

The subopercle of all the genera analyzed in this study is flat and triangular. The dorsal margin of the subopercle abuts the ventral margin of the opercle medially. The subopercle of all trichiurids is poorly ossified and has a strongly fimbriated or splintered ventral margin, whereas the ventral margin of the subopercle in the outgroup genera is mostly complete, and fimbriations, if present, are extremely reduced and restricted to the posterodorsal corner of the bone.

Character 3. The fimbriations on the posteroventral corner of the subopercle in the trichiurid genera *Lepturacanthus* and *Trichiurus* are longer than the preceding ventral ones. Thus, the contour formed by the ventral margin of the subopercle and the posteroventral corner of the opercle in these two genera appears to be slightly concave (Fig. 7I, K). Tucker (1956) used this character to group these two genera into his subfamily Trichiurinae. All the other trichiurids and the outgroups have a subopercle which, together with the opercle, forms a convex ventral margin.

Character 4. The outgroups and trichiurids are characterized by the presence of an anterodorsal articular process on the subopercle. In the outgroups, the articular process extends dorsally at a right angle to the dorsal margin of the subopercle and articulates mainly with the anteroventral corner of the opercle (Fig. 9A). A much smaller anterior projection on the articular process articulates with the interopercle. All trichiurids possess an articular process that extends anteriorly, articulating mainly with the posterodorsal corner of the interopercle (Fig. 9B). The articular process is short in *Aphanopus*, *Benthodesmus*, and *Lepturacanthus*, whereas it is longer and more pointed in other trichiurids. The degree of elongation of the anterodorsal process seems to vary in a continuous gradient from pointed to rounded and is difficult to categorize.

Interopercle

The interopercle is triangular and poorly ossified. The dorsal margin is characterized by a shallow lat-

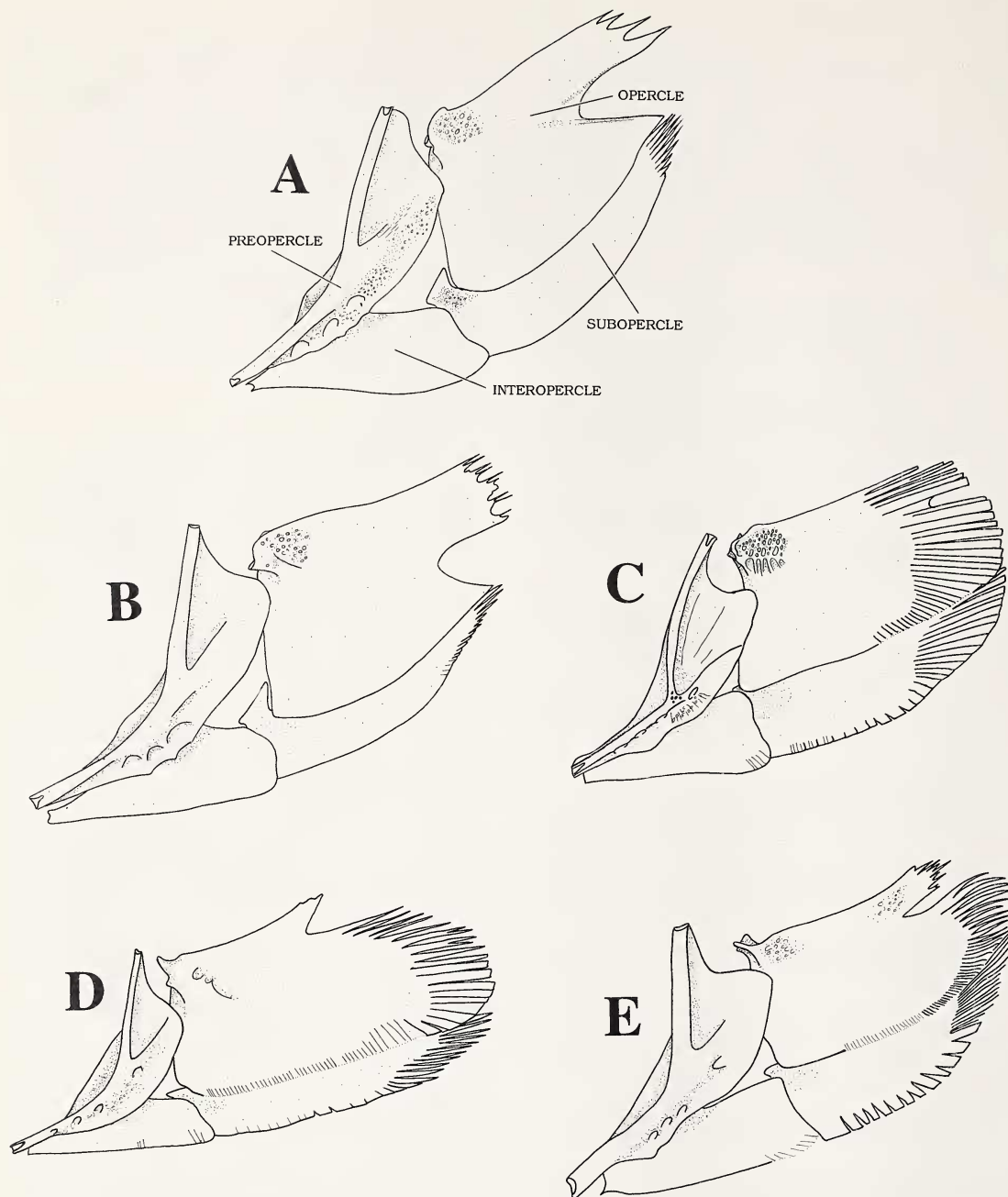


Figure 7. A-E. Lateral view of the left opercular series: (A) *Diplospinus multistriatus*; (B) *Paradiplospinus antarcticus*; (C) *Aphanopus arigato*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*.

eral fossa, which serves as a facet for the ventral portion of the posterior wing of the preopercle. Posteriorly, the margin of the interopercle overlaps the anterior margin of the subopercle laterally. The posterodorsal corner of the interopercle articulates with the anterodorsal articular process of the subopercle. Medially, the interopercle has a small anterodorsal fossa that articulates with the posterior

corner of the epihyal and the interhyal. The interopercle is similar among the species studied and differs only slightly in its overall shape.

Preopercle

The preopercle is crescent-shaped with a longitudinal lateral-line canal on the anterior margin and

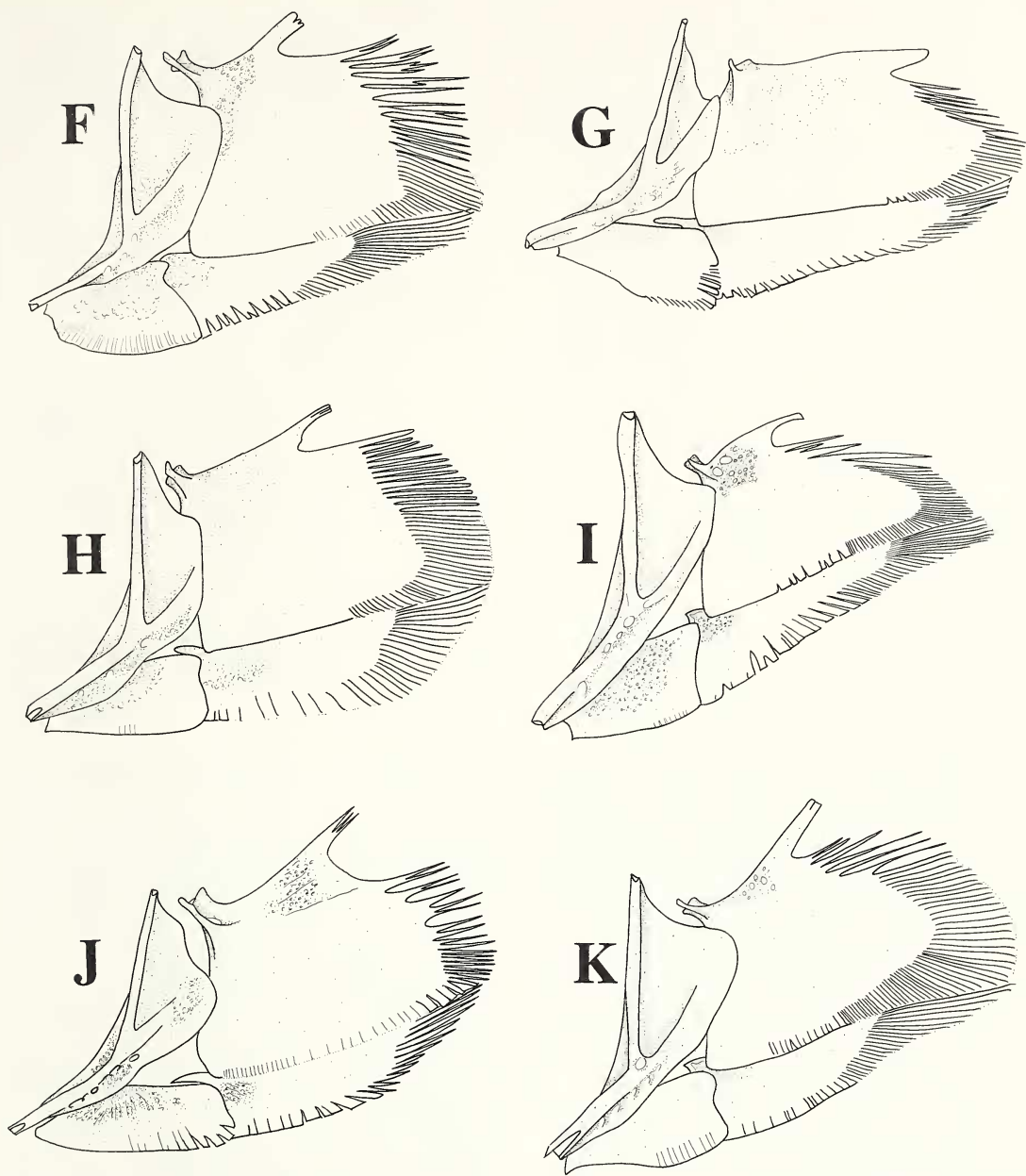


Figure 7. F-K. Lateral view of the left opercular series: (F) *Eupleurogrammus glossodon*; (G) *Evoxymetopon taeniatus*; (H) *Lepidopus fitchi*; (I) *Lepturacanthus savala*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.

a posterior strut on the dorsal half of the bone. The canal and the strut converge in the shape of a "Y." The anterior longitudinal canal carries the preopercular branch of the laterosensory canal system (Coombs et al., 1987), which it receives from a lateral pore on the pterotic. This preopercular canal exits the preopercle at the anteroventral tip to enter the articular bone. As it passes along the preopercle, the preopercular canal opens laterally through sensory pores. The preopercle is the most heavily

ossified bone in the opercular series. The posterior wing of the preopercle is less ossified than the central axis, and it overlays the anterior margin of the opercle and a shallow, dorsolateral fossa on the interopercle.

The posterior margin of the preopercle of all adult trichiurids is smooth and devoid of spines. Russo (1983) noted the variability in the posteroventral margin of the preopercle of gempylid genera. He indicated that the preopercular margin of

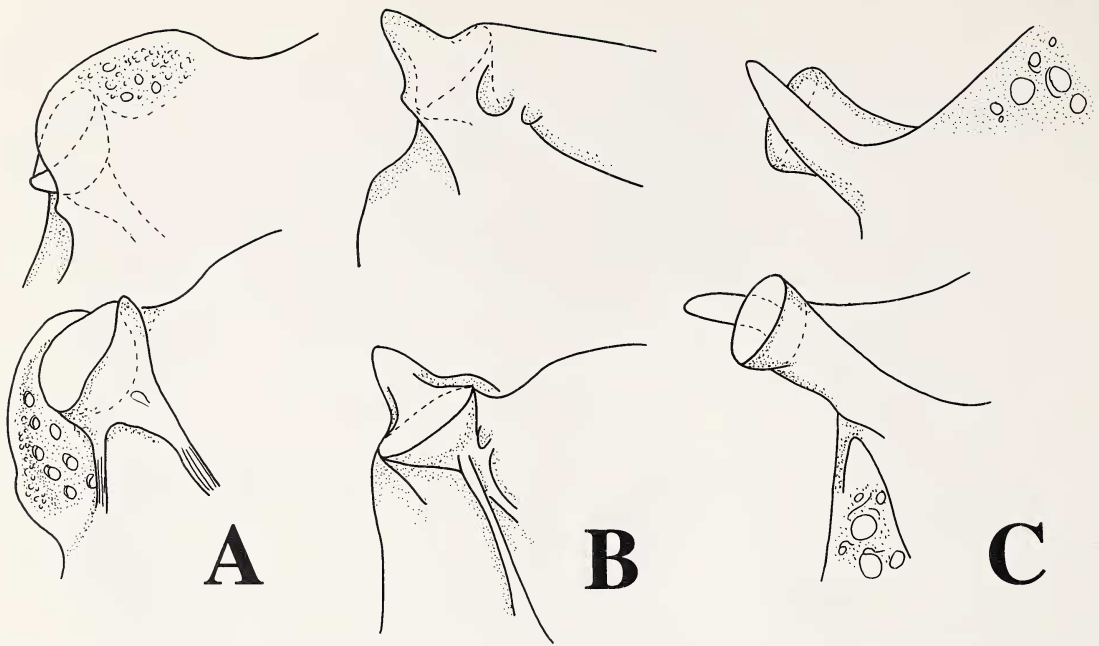


Figure 8. Lateral (top) and medial (bottom) views of the lateral process on the articular head of the left opercle: (A) *Diplospinus multistriatus*; (B) *Assurger anzac*; (C) *Trichiurus lepturus*.

the gempylids can be smooth (*Diplospinus*) or serrate (*Paradiplospinus*), have ventrally or dorsally directed spines (*Gempylus* and *Nesiarchus*), or be irregular in shape because of poor ossification. In some cases, the presence or absence of spines is difficult to evaluate because their recognition depends on the degree of ossification or development. For example, Russo (1983) noted the presence of small spines in *Paradiplospinus*, but concluded that they could be interpreted as serrations because of their poor development. Russo (1983) omitted this character from his analysis because of the difficulty in its interpretation.

Character 5. The preopercle of the outgroups *Gempylus* and *Nesiarchus* bears a convex posterodorsal margin. Russo (1983: character 48) identified the presence of a slightly concave posterodorsal margin on the preopercle as a synapomorphy of his gempylid clade comprising *Diplospinus* and *Paradiplospinus*. All trichiurids examined in this study share this feature. Because of the presence of a convex posterodorsal margin in the preopercle of all gempylids, except *Diplospinus* and *Paradiplospinus*, I agree with Russo (1983) and consider the presence of a concave posterodorsal margin as the derived condition.

CIRCUMORBITAL SERIES

The circumorbital series is a group of poorly ossified, small bones that carry the infraorbital branch of the lateral sensory canal system. Russo (1983) indicated that the numbers of left circumorbital el-

ements present in the gempylids *Diplospinus multistriatus*, *Gempylus serpens*, *Nesiarchus nasutus*, and *Paradiplospinus gracilis* (Brauer 1906) were 26, 29, 21, and 21, respectively. However, he noted that the number of circumorbitals varied not only within species but also between sides of the same specimen. Jollie (1986) indicated that hypotheses of homology concerning the infra- and postorbitals (excluding the lachrymal and jugal) are impossible because of the variation in the number of elements, as well as the arbitrariness of their recognition.

Character 6. All of the circumorbital series of the gempylids examined by Russo (1983: character 35) are continuous, except those of *Diplospinus* and *Paradiplospinus*, which have a short gap separating the first infraorbitals from the posterior circumorbitals (Fig. 10A, B). Russo (1983) considered the condition present in *Diplospinus* and *Paradiplospinus* as a synapomorphy uniting these two genera. A further derived condition, as explained by Johnson (1986: character 27), is present in the trichiurids, which have an extremely reduced circumorbital series (only the lachrymal and jugal are present, Fig. 10C–K). Although this character appears equivocal at the outgroup node in this study, I agree with Russo (1983) and Johnson (1986) in their polarization of the character states.

Lachrymal

The lachrymal constitutes the largest element of the circumorbital series. The ventral wing of the lachrymal is poorly ossified and membranous. The

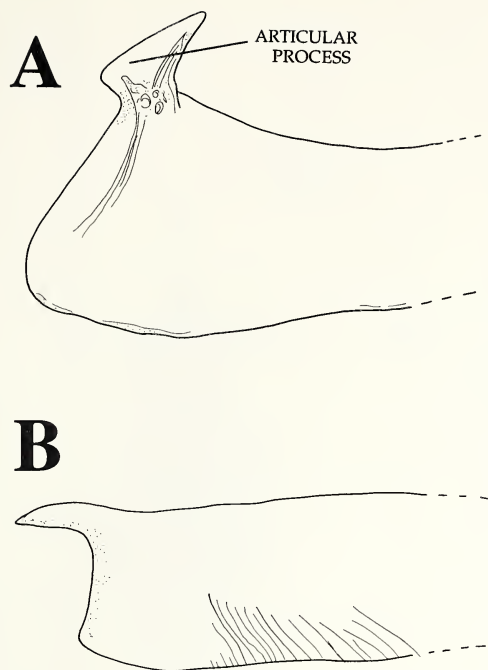


Figure 9. Lateral view of the articular process of the left subopercle: (A) *Paradiplaspinus antarcticus*; (B) *Lepidopsetta altifrons*.

poorly ossified ventral margin of this wing is fimbriated or splintered in the trichiurids. The latter character state was included by Johnson (1986) as part of his character complex 26. I do not consider this condition to be independent of that present in some of the opercular series (character 1). All trichiurids are characterized by a lachrymal with an extremely large ventral wing that completely covers the descending arms of the maxilla and premaxilla and in some cases extends past the ventral margin of the premaxilla. This character was recognized and used by Regan (1909) to define his family Trichiuridae. In the outgroups, the ventral wing does not cover the descending arms of the maxilla and premaxilla completely, and the ventral margin of the wing is complete. Matsubara and Iwai (1952) noted that the maxilla in *Gempylus* is largely hidden by the infraorbital membrane. However, variation in the extent of the ventral wing is continuous and the character is not included in the analysis since its categorization into objective states is difficult.

The ventral wing of the lachrymal is joined to a dorsal, longitudinal lateral-line canal. A perpendicular dorsal process of this longitudinal canal divides it into an anterior and a posterior section and forms the articular process that joins the lateral ethmoid. All the outgroups and trichiurids are characterized by articular processes that are elongate and pointed.

Character 7. In the trichiurids *Lepturacanthus* and *Trichiurus*, the ventral wing of the lachrymal becomes separated from the longitudinal, dorsal lateral-line canal at its anterior and posterior tips. The fimbriations in the anterior and posterior margins of the ventral wing of *Lepturacanthus* and *Trichiurus* extend vertically and are almost perpendicular to the dorsal, longitudinal lateral-line canal. Thus, *Lepturacanthus* and *Trichiurus* have a ventral wing on the lachrymal that appears quadrilateral (Fig. 10I, K). The rest of the trichiurids and all outgroups, except *Gempylus*, have a lachrymal in which the anterior and posterior portions of the ventral wing are connected to the anterior and posterior tips of the dorsal, longitudinal lateral-line canal. In *Gempylus* and *Tentoriceps*, the anterior margin of the ventral wing seems to become slightly separated before its anterior tip. However, this condition is not comparable to that in *Lepturacanthus* and *Trichiurus*, where the anterior tip of the dorsal, longitudinal lateral-line canal extends free of the ventral wing for a longer distance. In the outgroups and the rest of the trichiurids, the fimbriations in the anterior and posterior portions of the ventral wing of the lachrymal are not perpendicular to the dorsal, longitudinal lateral-line canal, and the ventral wing appears ovoid (Fig. 10A–H, J).

Character 8. The posterodorsal angle between the articular process and the posterior section of the dorsal, longitudinal lateral-line canal is strengthened by a plate-like ossification. This plate-like ossification extends posteriorly and terminates before or above the posterior pore of the dorsal, longitudinal lateral-line canal in the outgroups and the trichiurids *Aphanopus* and *Benthodesmus* (Fig. 10A–C, E). In the rest of the trichiurids this plate-like ossification extends past the posterior pore of the longitudinal, dorsal lateral-line canal and ends above the jugal (Fig. 10D, F–K).

Jugal

The jugal is the next bone, posterior to the lachrymal. Russo (1983: character 33) indicated that in all gempylids, except *Lepidocybium* and *Ruvettus*, the articulation between the lachrymal and the jugal is weak and the two elements are not in contact. Although the outgroup specimens analyzed in this study, except *Gempylus* where the jugal and lachrymal are separated, have a weak articulation between the jugal and lachrymal, these elements remain in contact with each other. The contact between the first two infraorbitals seems to be completely lost only in the trichiurids and *Gempylus*. The degree of separation between the lachrymal and the jugal is difficult to interpret and appears to be highly variable. Jollie (1986) considered the term jugal as useful only in its positional reference. Problems of interpretation of the homology of this bone may be, in part, a result of the probable separation of free lateral-line canal units from the posterior end of the lachrymal.

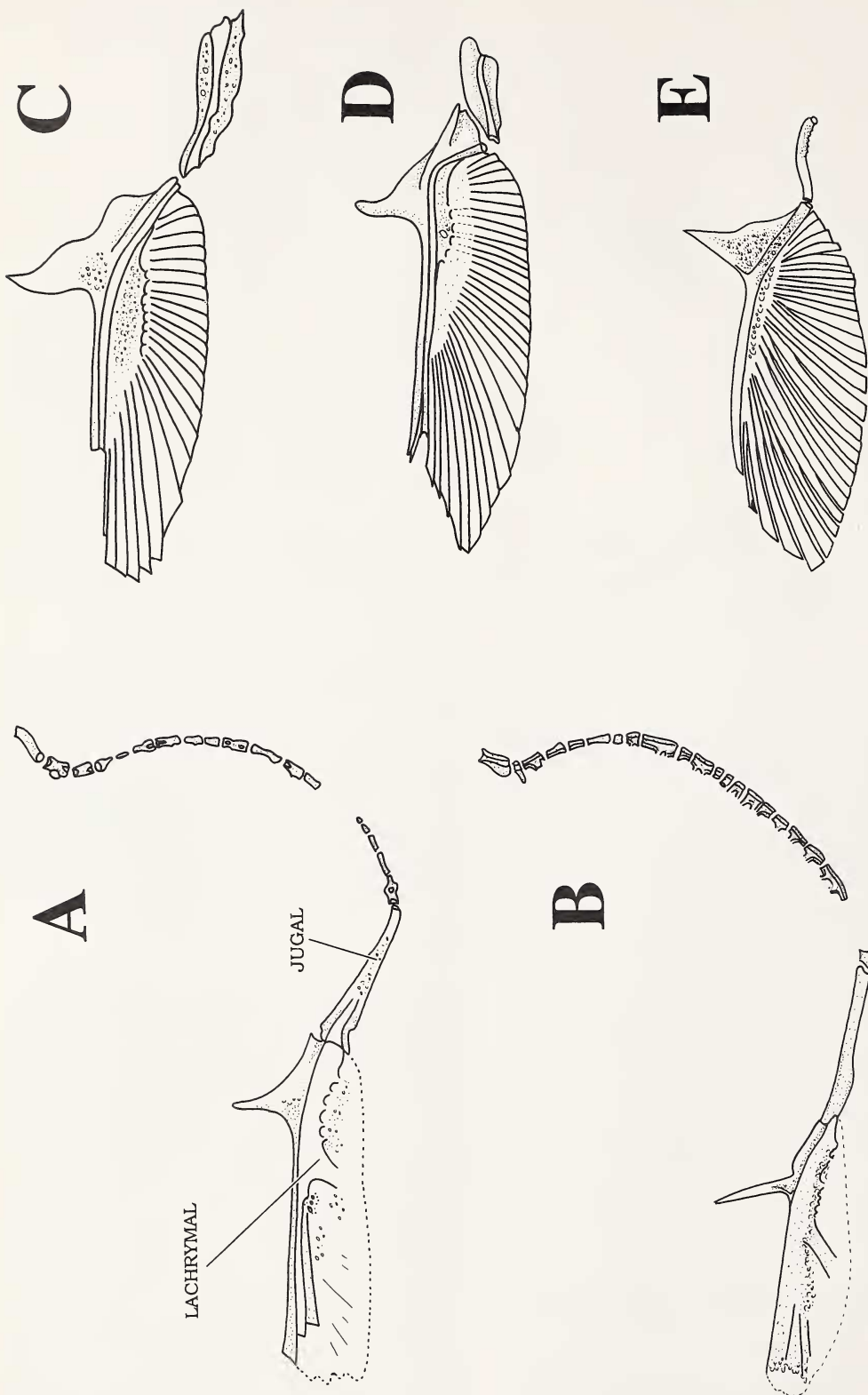


Figure 10. A-E. Lateral view of the left circumorbital series: (A) *Diplospinus multistriatus*; (B) *Paradipllospinus antarcticus*; (C) *Assurger anzac*; (D) *Aphanopus arigato*; (E) *Benthodesmus tenuis*.

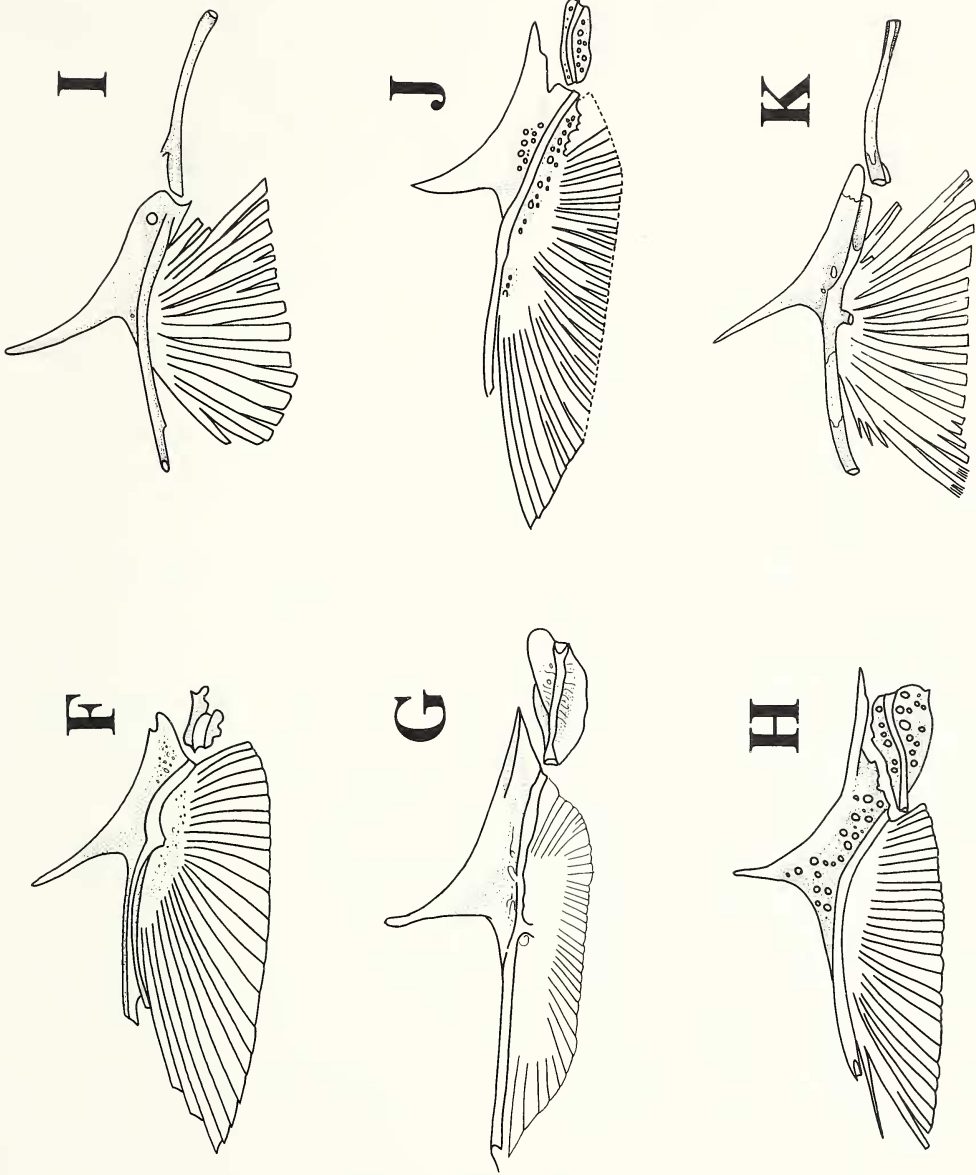


Figure 10. F-K. Lateral view of the left circumorbital series: (F) *Eupleurogrammus glossodon*; (G) *Evoxymetopon taeniatius*; (H) *Lepturacanthus savala*; (I) *Lepidopus fitchii*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.

The jugal in the gempylids *Diplospinus*, *Nesiarchus*, and *Paradiplospinus* and the trichiurids *Aphanopus carbo*, *Benthodesmus*, *Lepturacanthus*, and *Trichiurus* is a simple tube with ventral and dorsal laminar ossifications that are extremely reduced (i.e., they do not extend along the entire length of the bone) or absent. *Gempylus* and the trichiurids *Aphanopus arigato*, *Assurger*, *Eupleurogrammus*, *Evoxymetopon*, *Lepidopus*, and *Tentoriceps* have a jugal with well-developed ventral and dorsal laminar extensions that extend along the whole or most of the length of the bone. However, the condition is variable within genera (e.g., *Aphanopus*) and difficult to interpret since it depends on the size and degree of ossification of the specimens. The cleared and stained specimen of *Aphanopus arigato* analyzed in this study had well-developed laminar ossifications in the jugal, whereas a smaller specimen of *Aphanopus carbo* lacked the condition. Some specimens of *Diplospinus* and *Trichiurus* have small laminar ossifications anteriorly. Other specimens seem to show the presence of membranous dorsal and ventral extensions, which are not yet ossified.

Postorbital Ossification

Character 9. *Assurger*, *Benthodesmus*, *Evoxymetopon*, *Lepidopus*, *Lepturacanthus*, and *Trichiurus* have a paired, ossified element suspended in the adipose tissue of the posterior margin of the orbit (Fig. 11). The postorbital ossification in *Lepturacanthus* and *Trichiurus* is large, thick, and strongly ossified, whereas in *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* it is small, thin, and poorly ossified. This element does not appear to have a lateral-line canal. Laterally, it appears as a crescent-shaped ossification, but upon close examination it is plate-like and extends medially as a small postorbital shelf. The posterior face of the postorbital ossification tends to be slightly convex, whereas the anterior face is concave. In anterior view, the postorbital ossification of *Lepturacanthus* and *Trichiurus* appears triangular. The shape of this element in *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* is quite variable and dependent on the size of the specimens. In *Evoxymetopon* and *Lepidopus* the postorbital ossification bears dorsal or ventral processes at the lateral or medial corners. The outgroups and the rest of the trichiurids lack postorbital ossifications. Johnson (1986), Senta (1975), and James (1961) mentioned the presence of these ossifications but did not attempt any hypotheses of homology. Senta (1975) and James (1961) described these ossifications as the dermosphenotic. Although the homology between the conditions observed in *Lepturacanthus* and *Trichiurus* and the rest of the trichiurids having a postorbital ossification is inconclusive, I include this character complex in the data matrix as a multi-state character.

JAWS

Johnson (1986) indicated that the scombroids are characterized by jaws with teeth that are peripherally ankylosed to the walls of a longitudinal crypt (tooth attachment Type 1 of Fink, 1981). He also indicated that tooth replacement within these longitudinal crypts occurs between the mature ankylosed teeth.

Accurate counts of the actual numbers of mature, ankylosed teeth in trichiurids are difficult because the old teeth are rapidly shed or resorbed after replacement and are easily lost in preserved specimens. There is no apparent systematic pattern of replacement, and within a species, two specimens of the same size may not correspond in their dental formula or arrangement of replacement and mature teeth. Soot-Ryen (1936) indicated that in *Aphanopus minor* Collett 1887 (= *A. carbo*), the number and placement of teeth vary considerably between individuals and so cannot be used as specific characters.

The trichiurids, as well as all the other scombroids, have teeth of reticulate or cancellous appearance internally when viewed in glycerin (Johnson, 1986). A longitudinal crypt extends along the dorsal margin of the dentary and the ventral margin of the premaxilla, serving as the base for a uniserial row of teeth in each of these bones. These teeth are mediolaterally flattened and triangular, with well-developed anterior and posterior cutting edges, except in the dentary of *Nesiarchus* where they are retrorse. Large specimens of *Nesiarchus* and the trichiurids *Lepturacanthus* and *Trichiurus* are distinct in that some of the anterior-most teeth in the longitudinal series of the dentary are barbed. The serial teeth of the trichiurids *Lepturacanthus* and *Trichiurus* have well-developed barbs at their points, whereas those of *Nesiarchus* have no barbs or are extremely reduced in some specimens.

Most trichiurids and outgroups have a pair of small fangs on the dentary (Fig. 12). These fangs are barbed and large in *Lepturacanthus* and *Trichiurus*. Some large specimens of *Lepidopus caudatus* and *Lepidopus fitchi* also bear reduced barbs on the dentary fangs. The condition is also variable within genera. For example, of the two species of *Eupleurogrammus*, only *E. glossodon* has dentary fangs (Nakamura and Parin, 1993).

A pair of small canine teeth on the premaxilla project forward and are visible from a dorsal aspect in *Lepturacanthus*. *Eupleurogrammus*, *Tentoriceps*, and *Trichiurus* also have a pair of small, anteriorly directed teeth on the premaxilla, but these are not visible in dorsal view. Nakamura and Parin (1993) noted the presence of two small canine teeth projecting forward on the premaxillary symphysis as a character that differentiates *Lepturacanthus* and *Trichiurus*. This character is dependent on the size of the specimens, and it is quite variable within genera.

All gempylids and trichiurids in this study had a

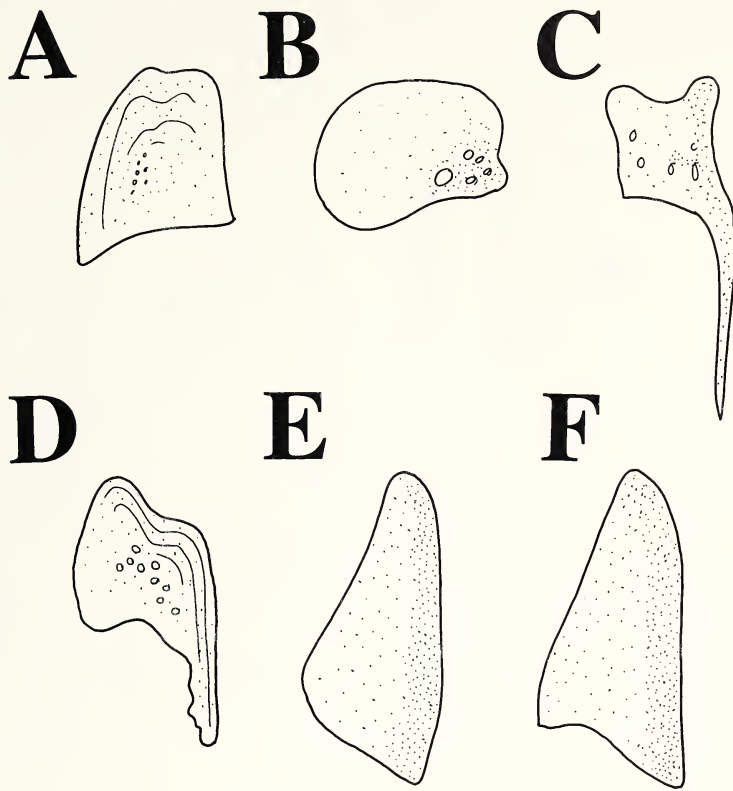


Figure 11. Anterior view of the left postorbital ossification: (A) *Assurger anzac*; (B) *Benthodesmus tenuis*; (C) *Evoxymetopon taeniatum*; (D) *Lepidopus caudatus*; (E) *Lepturacanthus savala*; (F) *Trichiurus lepturus*.

cluster of up to six fangs at the tip of the premaxilla. These teeth are not part of the longitudinal crypt and are rounder in cross section, larger, and stronger than those of the longitudinal series. Some of the teeth in this cluster are depressible. The anterior fangs in *Lepturacanthus* and *Trichiurus* have well-developed barbs. Some large specimens of *Eupleurogrammus*, *Lepidopus caudatus*, and *Nesiarchus* may also bear reduced barbs on their premaxillary fangs. The presence of barbs might represent a more derived condition than that noted by Russo (1983: character 37), where the gempylids *Gempylus*, *Nealotus*, *Nesiarchus*, *Promethichthys*, *Rexea*, and *Thyrssitoides* are characterized by having fangs with an extended, flattened cutting edge on the posterodistal surface. He considered that the condition of simple pointed fangs found in *Diplospinus*, *Paradiplospinus*, and the rest of the gempylid genera represented the plesiomorphic state. However, the presence of barbs on the premaxillary fangs is variable within genera and species. For example, Nakamura and Parin (1993) reported that *Trichiurus auriga* Klunzinger 1884 and most specimens of *Eupleurogrammus* lack barbs on the premaxillary fangs.

Character 10. All of the species analyzed in this study have serial teeth with smooth edges, except

for those in the outgroup *Gempylus* and the trichiurid *Aphanopus*, which have serrate edges. The premaxillary fangs of large specimens of *Aphanopus* and the outgroup *Gempylus* are also serrate. Maul (1953) reported the presence of minute serrations along the anterior margin of the premaxillary canines of *Benthodesmus simonyi*. The specimen of *B. simonyi* analyzed in the present study (USNM 292768) has only slight irregularities along the margins of the fangs and serial teeth. These irregularities are not comparable to the serrations of *Aphanopus* or *Gempylus*. Russo (1983) noted that among the gempylids only *Gempylus* and *Thyrssites* have serrate edges on their fangs and serial teeth. However, *Gempylus* has serrations in both the posterior and anterior edges, whereas *Thyrssites* bears serrations only on the anterior edge of the fangs and the posterior edges of the serial teeth. Russo (1983: character 38) considered the presence of serrations on the premaxillary fangs as the apomorphic condition. I agree with Russo (1983), but extend the character to include the presence of serrations on the anterior and posterior edges of the fangs and the serial teeth as the apomorphic condition.

Lower Jaw

DENTARY. Posteriorly, the dentary is divided into a ventral and a dorsal arm (process). A large

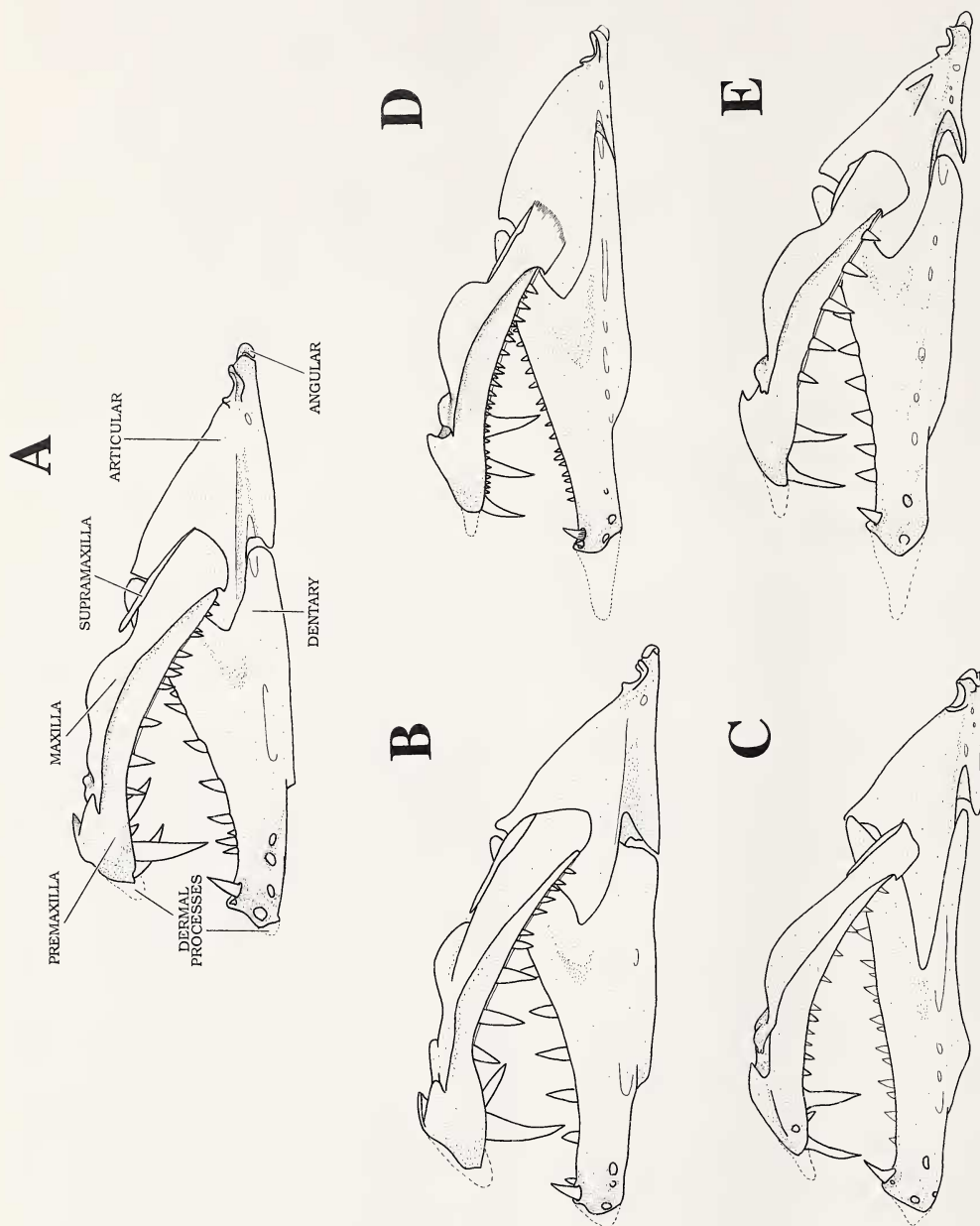


Figure 12. A-E. Lateral view of the left lower and upper jaw bones: (A) *Benthodesmus tenuis*; (B) *Diplospinus multistriatus*; (C) *Aphanopus arigato*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*.

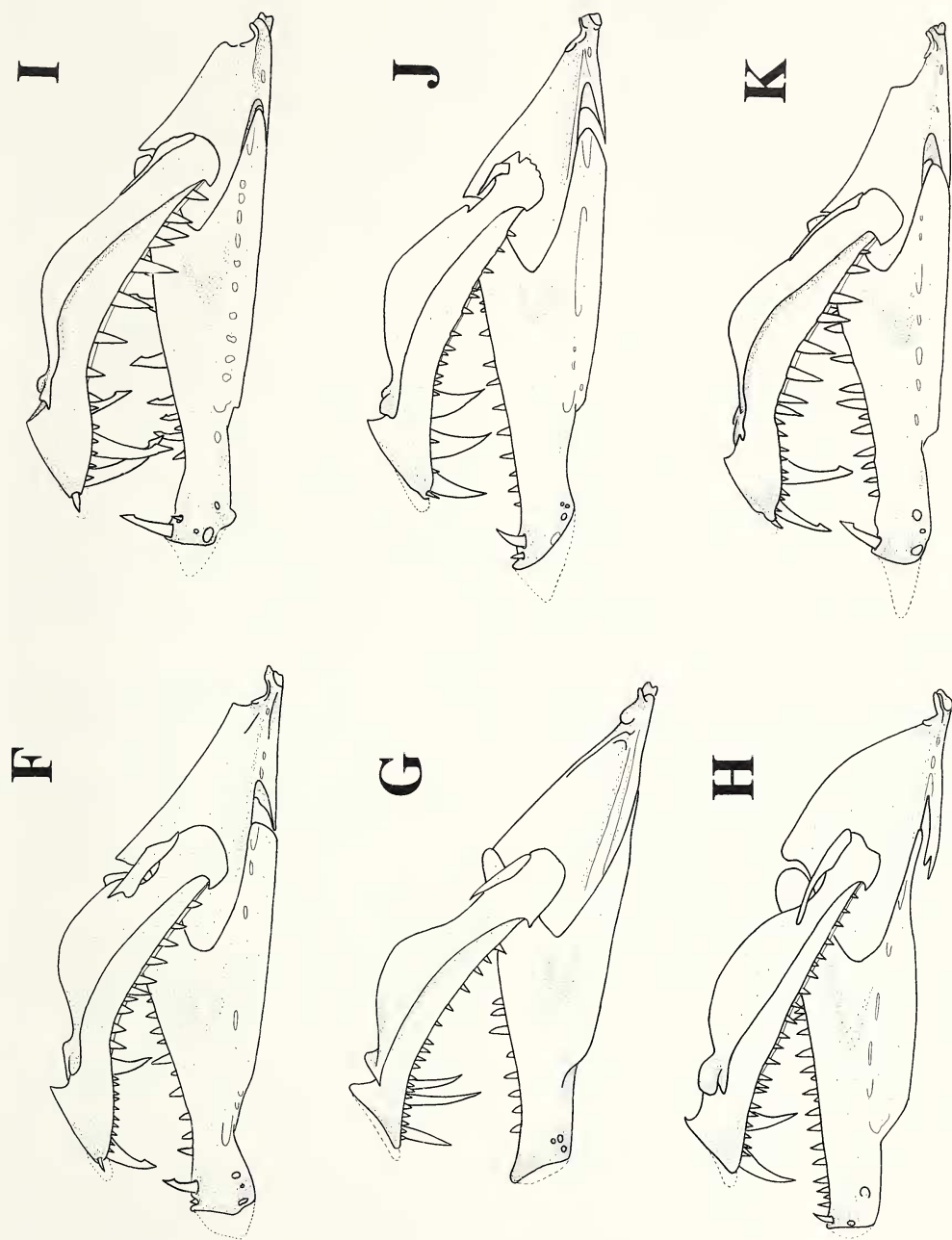


Figure 12. F–K. Lateral view of the left lower and upper jaw bones: (F) *Eupleurogrammus glossodon*; (G) *Euxymetopon taeniatus*; (H) *Lepidopus fitchi*; (I) *Lepturacanthus savala*; (J) *Tentoriiceps cristatus*; (K) *Trichiurus lepturus*.

anteromedial fossa between the two arms accepts the anterior process of the articular. The dentary is sutured anteriorly with the tip of Meckel's cartilage at the mandibular symphysis.

Russo (1983) noted that the presence of a fleshy conical process at the mandibular symphysis is always correlated with the occurrence of a similar structure at the premaxillary symphysis, and he considered it apomorphic among gempylids. However, there is some disagreement among authors about the presence or absence of these conical processes in the gempylids *Diplospinus* and *Nealotus*. Russo (1983) reported them in *Nealotus*, whereas Parin and Becker (1972) and Nakamura and Parin (1993) did not. Russo (1983) also characterized *Diplospinus* by the absence of such processes, whereas Nakamura and Parin (1993) noted their presence only at the premaxillary symphysis. The confusion may be a result of the reduced condition of these conical processes in some genera. The mandibular symphyses of all the trichiurids and the outgroups analyzed in this study have an anteriorly directed, external conical process (dermal process of Nakamura and Parin, 1993). In the outgroups *Diplospinus* and *Paradiplospinus*, the trichiurid *Evoxymetopon*, and some species of *Lepidopus*, this conical process is extremely reduced, and it is easily overlooked, except in cleared and stained specimens examined through transmitted light. This conical process has been described by some authors (Tucker, 1956; James, 1961; Parin and Becker, 1972; Russo, 1983) as a cartilaginous projection, but it does not stain with alcian blue.

ARTICULAR. The articular forms the posterior angle of the lower jaw and couples it to the palatoquadrate. Anteriorly, a large, triangular process fits into the anteromedial fossa of the dentary. Besides this anteromedial process, the articular also bears a dorsal, a ventral, and a posterior process. The dorsal and ventral processes are anteriorly directed and shorter than the anteromedial triangular process of this bone. Their tips abut or approach the posterodorsal and posteroventral arms of the dentary. The posterior process of the articular is hook-shaped, and it bears a transverse dorsal articular fossa for articulation with the quadrate. The ventral corner of this posterior process bears medial and lateral depressions in which the angular fits. The morphology of this bone is similar in all of the species studied.

ANGULAR. The angular is a small hook-shaped bone that fits on the posteroventral corner of the articular. A small arm fits laterally on the posteroventral corner of the articular, whereas a longer arm curves around and fits into a depression on the medial side. In all the outgroups and the trichiurids this medial arm extends anteriorly along the medial face of the posteroventral corner of the articular as an elongate, tubular process. The extent of the elongation of the medial arm is variable among genera. In some genera the medial arm extends dorsally, forming a wider, plate-like process that covers

most of the medial face of the posteroventral corner of the articular. The shape of the medial arm of the angular is quite variable and it is difficult to categorize into objective character states.

Upper Jaw

PREMAXILLA. All the trichiurids and the outgroups have an external dermal process at the premaxillary symphysis. As indicated earlier in the description of the dentary bone, this structure is considered together with the presence of a dermal process at the mandibular symphysis. The premaxillary dermal process tends to be smaller than that present at the dentary. This dermal process in the trichiurids is also smaller than that of the outgroups *Diplospinus* and *Paradiplospinus*.

All scombroids are characterized by having a nonprotrusible upper jaw, with the premaxilla strongly attached to the maxilla and the ethmovomerine region of the neurocranium (Collette et al., 1984: character 19; Johnson, 1986: character 9).

A small, ascending process extends dorsally from the anterior tip of the premaxilla. The ascending process abuts the rostral cartilage, which provides a pivot point for the dorsoventral rotation of the premaxilla (Johnson, 1986). The trichiurids are characterized by the presence of a shortened, ascending process on the premaxilla. Russo (1983: character 39) indicated that the gempylids also share the presence of a short, ascending process of the premaxilla.

Posterior to the ascending process, a small, dorsal process serves as the articular condyle for the maxilla. The descending arm of the premaxilla extends posteriorly and medially to the maxilla. The posterior-most margin of the premaxilla does not extend past the descending arm of the maxilla. Russo (1983: character 40) also found that all the gempylids were characterized by a posterior premaxillary arm that does not extend beyond the descending arm of the maxilla.

MAXILLA. Anteriorly, the maxilla has a strong, rounded articular head that articulates with the palatoquadrate and the ethmovomerine region of the neurocranium. Ventrally, the articular head is also divided by a notch that accepts the articular condyle of the premaxilla.

Posterior to the articular head, the maxilla becomes narrow, forming a small dorsal depression that accepts the maxillary process of the palatine. The descending arm of the maxilla becomes wider as it extends posteroventrally and completely covers the descending arm of the premaxilla. Dorsally, the descending arm of the maxilla may expand into a dorsal ridge that serves as an attachment point for the adductor mandibulae. Russo (1983: character 42) indicated that all gempylids share the presence of a well-developed dorsal ridge that arches high above the dorsal margin of the maxilla. He also noted that a more derived state was present in the genus *Gempylus*, where the ridge is extremely

large and occupies about two thirds of the anterior half of the maxilla. All the trichiurids, except *Aphanopus*, *Lepturacanthus*, and *Trichiurus*, have well-developed dorsal ridges. The presence of a well-developed dorsal ridge on the maxilla is correlated with a dorsal notch formed between the dorsal ridge and the posterior margin of the maxilla. In those cases where the dorsal notch is present, the posterior margin of the maxilla is dorso-ventrally expanded. The extent of the dorsal ridge of the maxilla is quite variable, and this character cannot be easily categorized.

The posterodorsal corner of the maxilla accepts the posterior half of the supramaxilla, which extends anteriorly and sometimes reaches the posterior margin of the dorsal ridge. The posteroventral corner of the maxilla is hook-shaped and expands beyond the ventral margin of the descending arm of the premaxilla.

SUPRAMAXILLA. All the trichiurids, except *Eupleurogrammus*, and outgroups, except *Nesiarchus*, have an extremely reduced, splint-like supramaxilla. Russo (1983: character 43) considered the presence of a reduced splint-like supramaxilla as a derived condition uniting the gempylids *Diplospinus*, *Gempylus*, and *Paradiplospinus*. The trichiurid *Eupleurogrammus* and the outgroup *Nesiarchus* are characterized by having a much wider, well-developed supramaxilla. However, it is difficult to categorize the variation in the size of the supramaxilla into objective character states. In those trichiurids and gempylids having a well-developed dorsal notch on the descending arm of the maxilla (*Asurger*, *Benthodesmus*, *Diplospinus*, *Eupleurogrammus*, *Evoxymetopon*, *Gempylus*, *Lepidopus*, *Nesiarchus*, *Paradiplospinus*, and *Tentoriceps*), the supramaxilla originates laterally on a dorsal plate-like expansion of the posterior margin of the maxilla. In most cases, the supramaxilla extends anteriorly over the dorsal notch of the maxilla and its anterior half remains unattached. In *Eupleurogrammus* and *Lepidopus*, the anterior margin of the supramaxilla reaches and attaches to the dorsal ridge of the maxilla. The central part of the body of the supramaxilla remains free and unattached to the maxilla. The trichiurids *Aphanopus*, *Lepturacanthus*, and *Trichiurus* lack a well-developed dorsal notch, and the supramaxilla simply extends along the dorsal margin of the maxilla to which it attaches.

SUSPENSORIUM

Collette and Russo (1984) separated the bones of this series into the palatine and hyoid arches. The palatine arch consists of the palatine, ectopterygoid, endopterygoid, and metapterygoid. The hyoid arch includes the hyomandibula, symplectic, quadrate, and hyoid complex. I include the palatine and hyoid arches as part of the suspensorium (Fig. 13) but exclude the hyoid complex, which is discussed separately.

Hyomandibula

The hyomandibula has a cruciform dorsal process bearing three articular condyles. The anterior and dorsal condyles articulate with the hyomandibular fossa of the otic capsule (formed by the sphenotic, pterotic, and prootic), whereas the posterior condyle articulates with the articular fossa of the opercle.

The hyomandibula bears an elongate ventral arm with a prominent lateral ridge that is pointed at its dorsal tip. The lateral ridge serves as the attachment point to the anterior margin of the preopercle and the posterior margin of the metapterygoid. The angle between the anterior articular condyle and the ventral arm extends as a small plate that is fused medially and laterally to the dorsal corner of the metapterygoid. The morphology of the hyomandibula is similar among the taxa analyzed in this study.

Symplectic

The symplectic lies between the quadrate, metapterygoid, interhyal, and hyomandibula. It is tube-like, with the ventral half fitting along the postero-medial fossa of the quadrate. Anterodorsally, it has a plate-like extension that abuts the posteroventral corner of the metapterygoid medially. Posterodorsally, the symplectic of all trichiurids and the outgroups bear a spine-like extension that is covered by the posterodorsal process of the quadrate.

Quadrate

In the trichiurids, the quadrate joins the lower jaw to the rest of the suspensorium. It is triangular and bears a transverse mandibular condyle on the ventral corner that fits on the articular fossa of the articular bone. The anterior margin articulates with the ventral arm of the ectopterygoid, whereas the dorsal margin abuts the metapterygoid. Posteromedially, it bears a depression that accepts the ventral portion of the symplectic.

Character 11. The posterior margin of the quadrate is strongly ossified and bears a posterodorsal process. This process is elongate and extends well past the ventral margin of the metapterygoid in all outgroups and trichiurids, except *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*. In *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* the process is shorter and does not extend well past the ventral margin of the metapterygoid. The strong posterior margin serves as an attachment surface for the anteroventral arm of the preopercle.

Metapterygoid

Anteromedially, the metapterygoid articulates with the ectopterygoid and the endopterygoid. Medially along the posteroventral corner, an extremely shallow fossa accepts the anterodorsal plate-like extension of the symplectic. The dorsal corner is usually divided into a medial and a lateral extension that

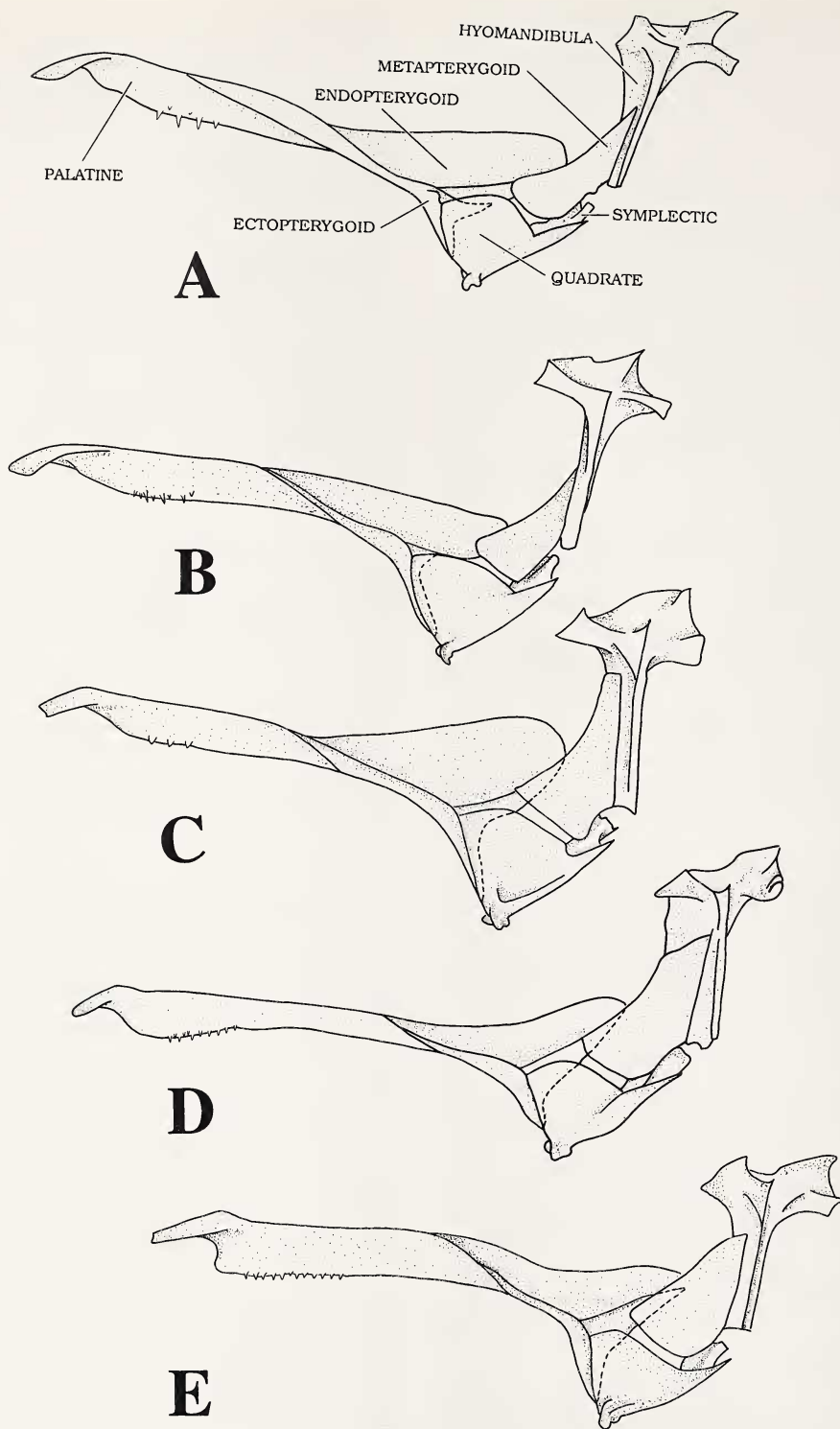


Figure 13. A-E. Lateral view of the left suspensorium: (A) *Diplospinus multistriatus*; (B) *Paradiplospinus antarcticus*; (C) *Aphanopus arigato*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*.

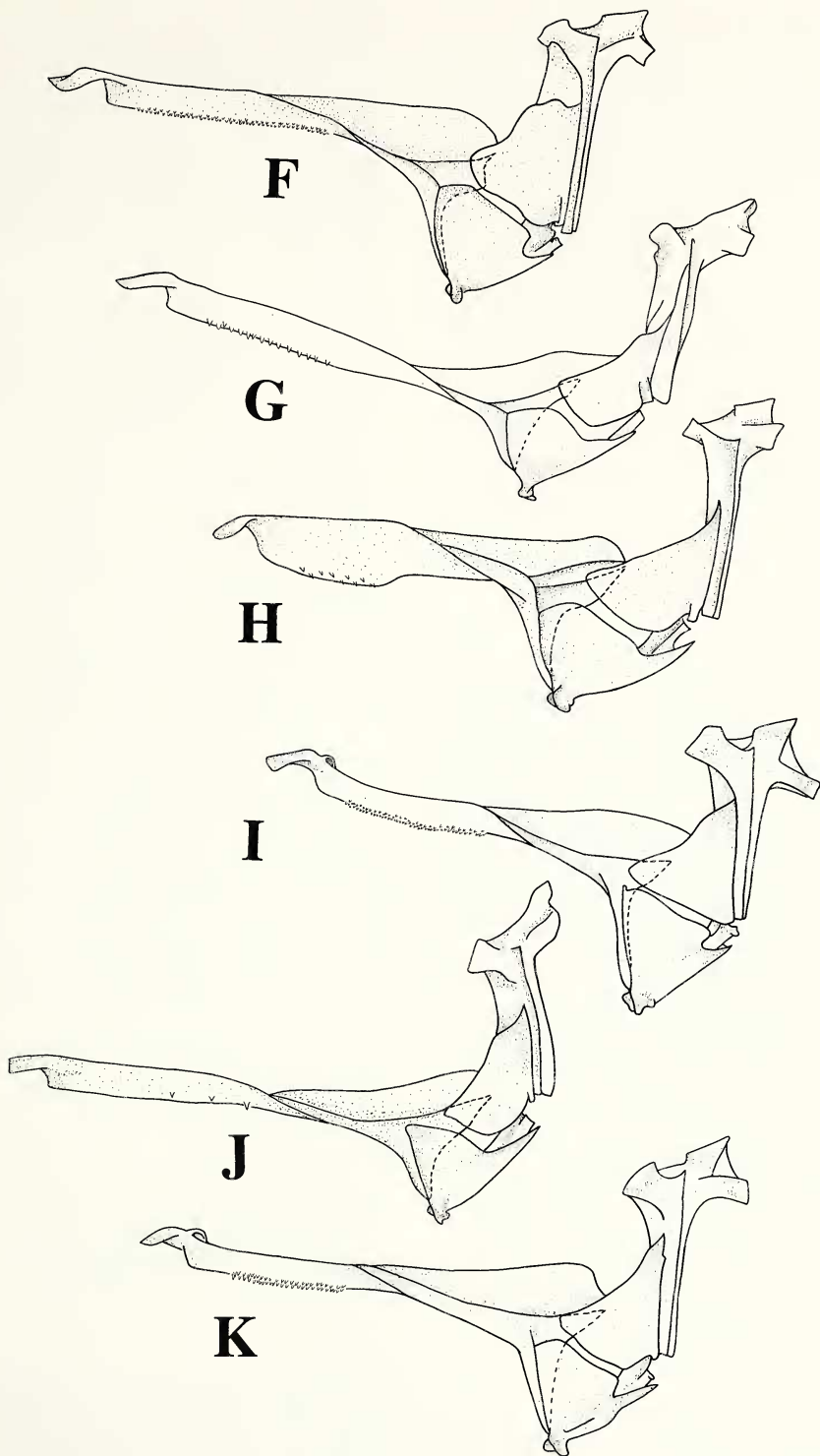


Figure 13. F–K. Lateral view of the left suspensorium: (F) *Eupleurogrammus glossodon*; (G) *Evoxymetopon taeniatum*; (H) *Lepidopus fitchi*; (I) *Lepturacanthus savala*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.

are strongly fused to the plate-like process at the angle between the anterior articular condyle and the ventral arm of the hyomandibula. All trichiurids and outgroups, except *Diplospinus* and *Paradiplospinus*, have well-developed lateral and medial processes on the metapterygoid. Russo (1983: character 45) noted that among the gempylids, only *Diplospinus*, *Lepidocybium*, and *Paradiplospinus* bear reduced lateral and medial processes on the metapterygoid. He noted that in these genera the dorsal margin of the metapterygoid appears to come to a single point, giving the bone a triangular appearance. All trichiurids, except some specimens of *Eupleurogrammus*, have a lateral process that comes to a point dorsally. However, the medial process is well developed and flat on its dorsal margin. The lateral shape of the metapterygoid is quite variable and difficult to categorize. This potential character is excluded from the present analysis, although it may prove to be useful in a future study of the gempylids and trichiurids in which its variation can be assessed more extensively.

Ectopterygoid

The ectopterygoid is composed of three or four arms (anterior, posteromedial, posterolateral, and ventral) that join this bone to the endopterygoid, palatine, quadrate, and sometimes metapterygoid. The posterior margin of the ventral arm articulates with the anterior margin of the quadrate. The anterior arm articulates with the lateral margin of the endopterygoid and fits into the longitudinal fossa of the palatine. *Nesiarchus* bears both a posterolateral and a posteromedial arm. These posterior arms articulate with the lateral margin of the endopterygoid and the anterodorsal corner of the quadrate. The posteromedial arm of *Nesiarchus* is much longer than the posterolateral arm, but it never reaches the anteroventral corner of the metapterygoid. In *Diplospinus*, *Gempylus*, *Paradiplospinus*, and all trichiurids only the posteromedial arm is present.

Character 12. In the outgroups, the posteromedial arm of the ectopterygoid articulates only with the lateral margin of the endopterygoid and the anterodorsal corner of the quadrate. All trichiurids are characterized by having a much longer posteromedial arm that extends up to and articulates with the anteroventral corner of the metapterygoid.

Endopterygoid

The lateral margin of the endopterygoid articulates anteriorly with the ectopterygoid and palatine and posteriorly with the metapterygoid. The endopterygoid of *Lepturacanthus* has a tuberculous patch anteriorly that bears a few small teeth. Although the anterior portion of the endopterygoid is better ossified than the posteromedial shelf, none of the outgroups or the rest of the trichiurids bear any teeth on this bone.

Palatine

The palatine attaches to the maxilla, the ethmoid, and the lateral ethmoid. Posteriorly, it bears a longitudinal fossa that serves as the surface for articulation with the anterior arm of the ectopterygoid and the lateral margin of the endopterygoid. Anteriorly, a hooked maxillary process fits above the dorsal depression that is present posterior to the articular head of the maxilla.

Character 13. A small, medially directed shelf that serves as an articulation point with the ethmoid is evident in the trichiurids and outgroups. Posterior to this small medial shelf, *Lepturacanthus* and *Trichiurus* also bear a well-developed, medially directed condyle at the dorsal corner between the maxillary process and the main body of the palatine. This condyle abuts the posterior margin of the palatal process of the ethmoid and is visible in lateral view.

Character 14. All of the outgroups and most of the trichiurids are characterized by having only a few teeth arranged uniserially and not covering the whole length of the ventral margin of the palatine. A few replacement teeth are usually present on the medial face of the palatine above and between the teeth in the main ventral series. Of the trichiurids, only *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* bear large numbers of teeth arranged in several rows and covering most of the length of the ventral margin of the palatine. In *Lepturacanthus* the condition is further modified and part of the medial side of the palatine is covered by a patch of small teeth. Maul (1953) noted that the palatine teeth in *Benthodesmus simonyi* are covered by a fleshy fold and that, in preserved specimens, the fold closes up so tightly that the presence of palatine teeth can be easily overlooked. The case is similar for the preserved specimens of the other trichiurid genera, which may explain previous reports of the absence of palatine teeth in some taxa. Tucker (1956) noted the difficulty in finding the palatine teeth in trichiurids and suggested that reports on their absence should not be taken too seriously.

HYOID COMPLEX

The hyoid complex is composed of a series of bones that articulate with the suspensorium and support the branchiostegal rays (Fig. 14).

Interhyal

The interhyal connects the hyomandibula to the epihyal. It is a small, cylindrical bone that is usually constricted in the middle and expanded at the tips. The morphology of this bone is similar among the taxa analyzed in this study.

Epihyal

The anterior margin of the epihyal is broad and articulates with the posterior margin of the ceratohyal. This anterior articulation includes blocks of

cartilage at the dorsal and ventral corners and suturing by way of odontoid processes in the middle. The posterior end of the epihyal narrows into an apex that bears a dorsal articular fossa for articulation with the interhyal. In the trichiurids, the three posterior-most branchiostegal rays attach laterally to the ventral margin of this bone. The morphology of the epihyal is similar among the taxa analyzed in this study.

Ceratohyal

The ceratohyal is a flattened bone that articulates posteriorly with the epihyal via blocks of cartilage and suturing by way of odontoid processes. The three anterior-most branchiostegals articulate medially on the ventral margin of this bone, whereas the fourth branchiostegal articulates laterally at the posteroventral corner. The hyoidean groove (Collette and Russo, 1984) runs longitudinally along the lateral face of the ceratohyal. A small slit on the hyoidean groove (the beryciform foramen of McAllister, 1968; or ceratohyal window of Collette and Chao, 1975) is present in *Eupleurogrammus*, *Evoxymetopon*, *Lepturacanthus*, *Tentoriceps*, and the outgroups *Diplospinus* and *Nesiarchus*. This interpretation differs from the observations of Russo (1983), who indicated that *Diplospinus* and *Nesiarchus* lack a ceratohyal window. Collette and Russo (1984) noted that the presence of a ceratohyal window within the Spanish mackerels (*Scomberomorus*: Scombridae) is quite variable.

Anteriorly, the ceratohyal articulates with the dorsal and ventral hypohyals by way of a layer of cartilage; the anteroventral corner of the ceratohyal projects anteriorly to articulate with the posteroventral notch of the ventral hypohyal.

Character 15. In *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*, the anterodorsal corner of the ceratohyal is pointed and extends anteriorly, abutting the dorsal margin of a layer of cartilage on the posterior margin of the dorsal hypohyal. All other trichiurids and outgroups lack this anterodorsal extension of the ceratohyal. In *Aphanopus* and some specimens of *Lepidopus fitchi*, the anterodorsal corner extends only slightly anteriorly, but it is not pointed and does not abut the dorsal margin of the cartilage of the dorsal hypohyal.

Dorsal Hypohyal

Anteriorly, the dorsal hypohyal articulates with the ventral hypohyal by suturing with odontoid processes, whereas posteriorly it articulates via a block of cartilage. The posterior margin articulates with the anterior margin of the ceratohyal by way of a layer of cartilage. The anterodorsal corner bears a medial projection that forms a symphysis with the opposing dorsal hypohyal, the anterior tip of the first basibranchial, and the posterior margin of the glossohyal.

The dorsal hypohyal of the trichiurid *Leptura-*

canthus is unique in that it bears teeth along the anterior half of its dorsal margin. These teeth are not part of a dermal plate or patch, and they are fused to the bony element. *Eupleurogrammus* bears longitudinal patches of teeth on the dorsal margin of the dorsal hypohyal. However, these tooth patches are part of the epithelium covering the bone and they are not fused to it.

Ventral Hypohyal

The ventral hypohyal is joined dorsally to the dorsal hypohyal. The posteroventral corner forms a longitudinal notch where the elongate anteroventral corner of the ceratohyal fits. The anteroventral corner bears a ventral projection that serves as the site for attachment of the ligaments coming from the articular head of the urohyal. The morphology of the ventral hypohyals is similar among the taxa analyzed in this study.

Glossohyal

The glossohyal is a median bone supporting the tongue. It is covered with flesh, and in the trichiurid *Eupleurogrammus*, it is unique in that it bears two elongate, dermal tooth patches dorsally. *Evoxymetopon* bears a few minute teeth on the lateral margins of the tongue. In both *Eupleurogrammus* and *Evoxymetopon*, the tooth patches are part of the flesh covering the glossohyal; they are not fused to the bone. All other trichiurids and outgroups analyzed in this study lack glossohyal teeth. Posteriorly, the glossohyal articulates with the anterodorsal corner of the dorsal hypohyals and the anterior margin of the first basibranchial. The dorsal face of this bone is flat or slightly concave in all the taxa analyzed in this study. Posteroventrally, the trichiurids and the outgroups, except *Gempylus*, have two lateral processes that converge anteriorly by way of a longitudinal keel. *Gempylus* bears these posteroventral processes but lacks a longitudinal keel.

Character 16. Russo (1983: character 51) considered the presence of quadrilateral posteroventral processes on the glossohyal as a derived condition among gempylids. I agree with Russo (1983) and consider the condition observed in *Nesiarchus* and most of the gempylids including *Lepidocybium*, in which the posteroventral processes do not appear quadrilateral, as the plesiomorphic state. He separated the condition observed in *Gempylus* as a different character. As indicated by Russo (1983: character 50), the posteroventral processes of the glossohyal in *Gempylus* are wing-like and have the distal ends pointing posteriorly. In this study, the conditions regarding the shape of the posteroventral processes are combined into a single multistate character. There are three derived conditions regarding the shape of the posteroventral processes relative to the state found in *Nesiarchus* and most of the gempylids: triangular, quadrilateral, and wing-like with the distal ends pointing posteriorly. *Diplospinus*, *Paradiplospinus*, and all trichiurids,

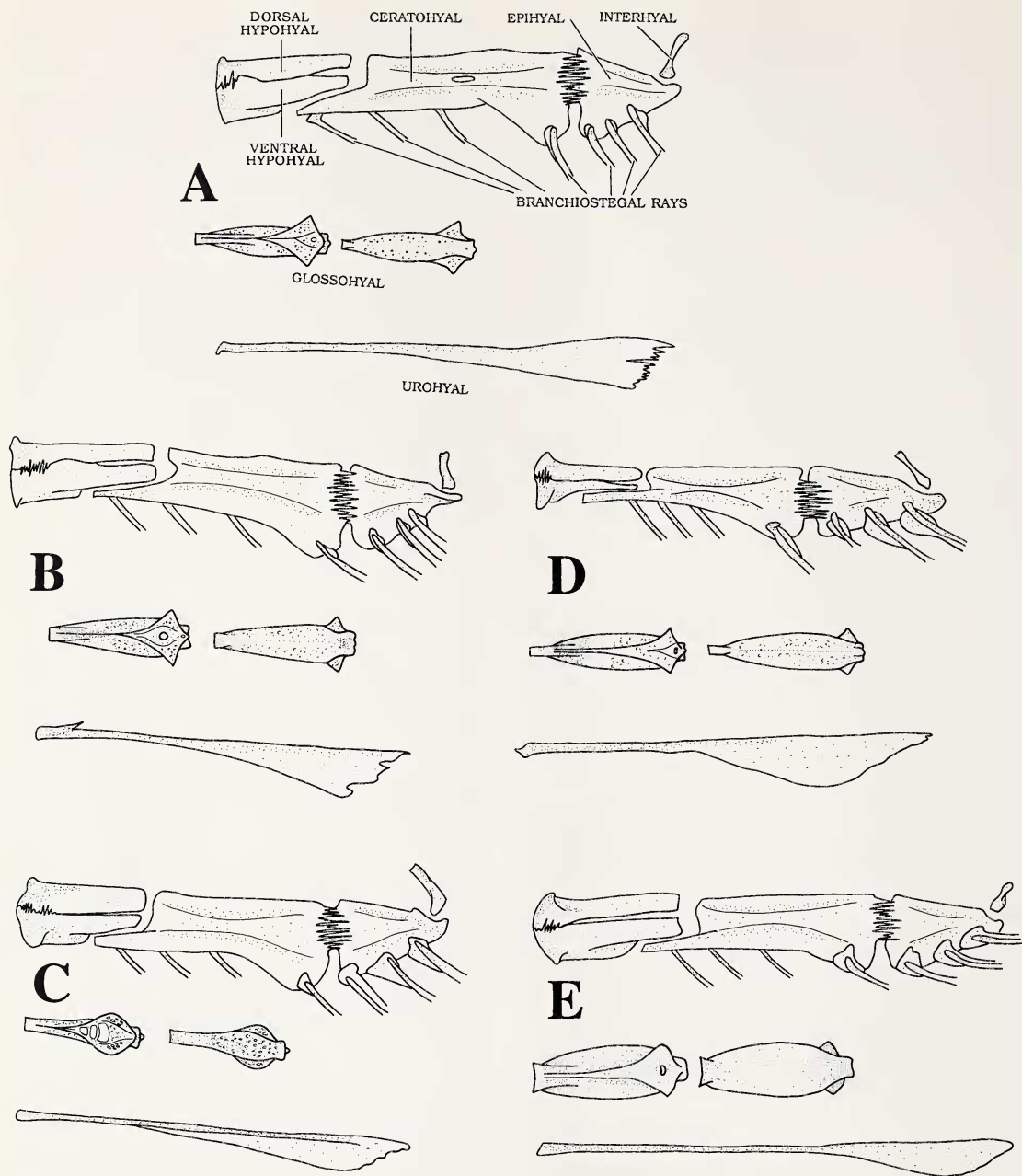


Figure 14. A-E. Lateral view of the left hyoid complex; the glossohyal is represented from left to right in ventral and dorsal views, respectively: (A) *Diplospinus multistriatus*; (B) *Paradiplospinus antarcticus*; (C) *Aphanopus arigato*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*.

except *Eupleurogrammus*, *Lepturacanthus*, *Tentoriiceps*, and *Trichiurus*, have ventral processes that appear quadrilateral in ventral view. The trichiurids *Aphanopus* and *Benthodesmus* bear posteroventral processes that appear quadrilateral, although not as pronounced as those in *Diplospinus* and *Paradiplospinus*. In some large specimens of *Aphanopus* and *Benthodesmus*, the lateral corners of the pos-

teroventral processes are rounded. The glossohyal of *Eupleurogrammus*, *Lepturacanthus*, *Tentoriiceps*, and *Trichiurus* bears triangular posteroventral processes. Furthermore, the posteroventral processes in *Gempylus* and *Nesiarchus* are located more anteriorly, leaving a well-developed posterior articular head in the glossohyal. In all trichiurids and the outgroups *Diplospinus* and *Paradiplospinus*,

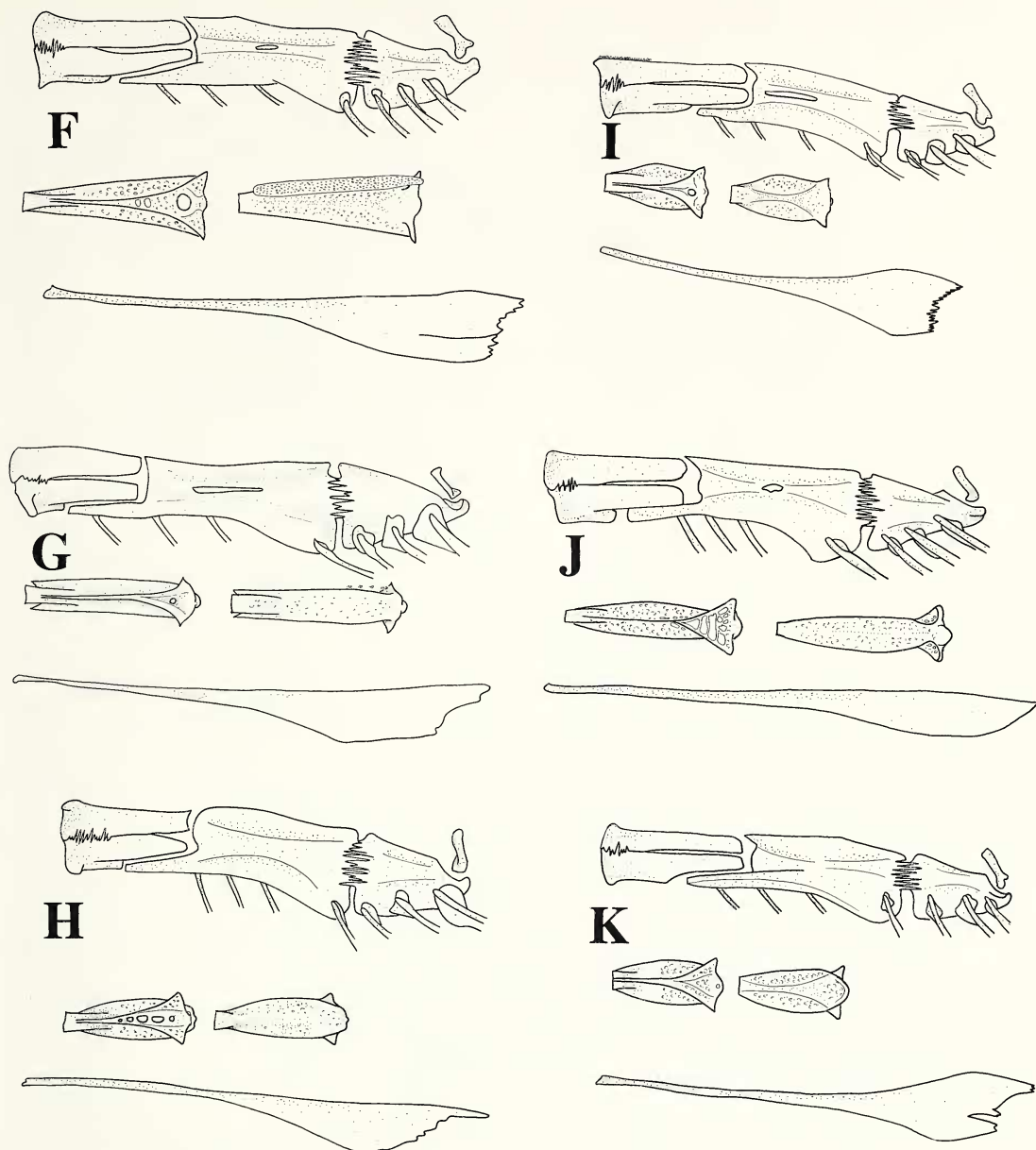


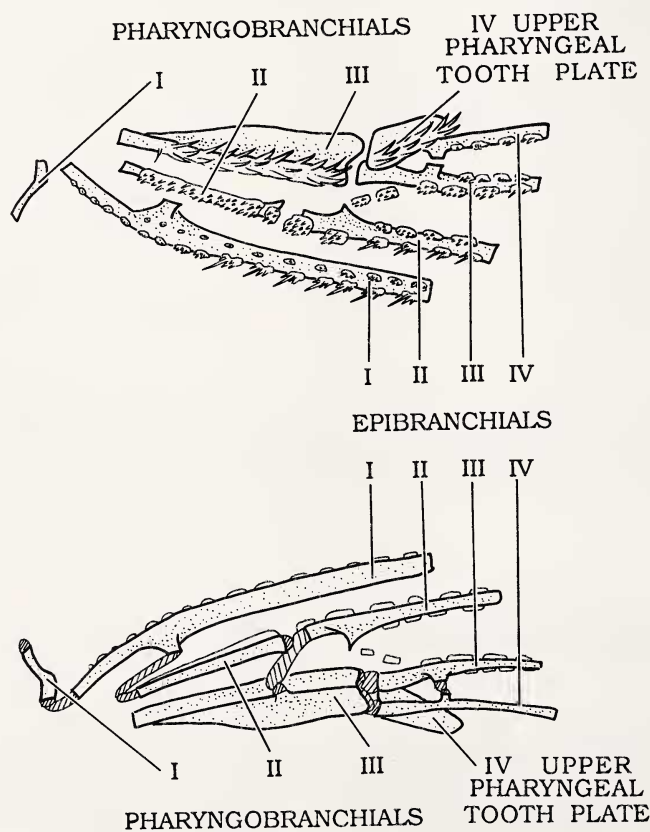
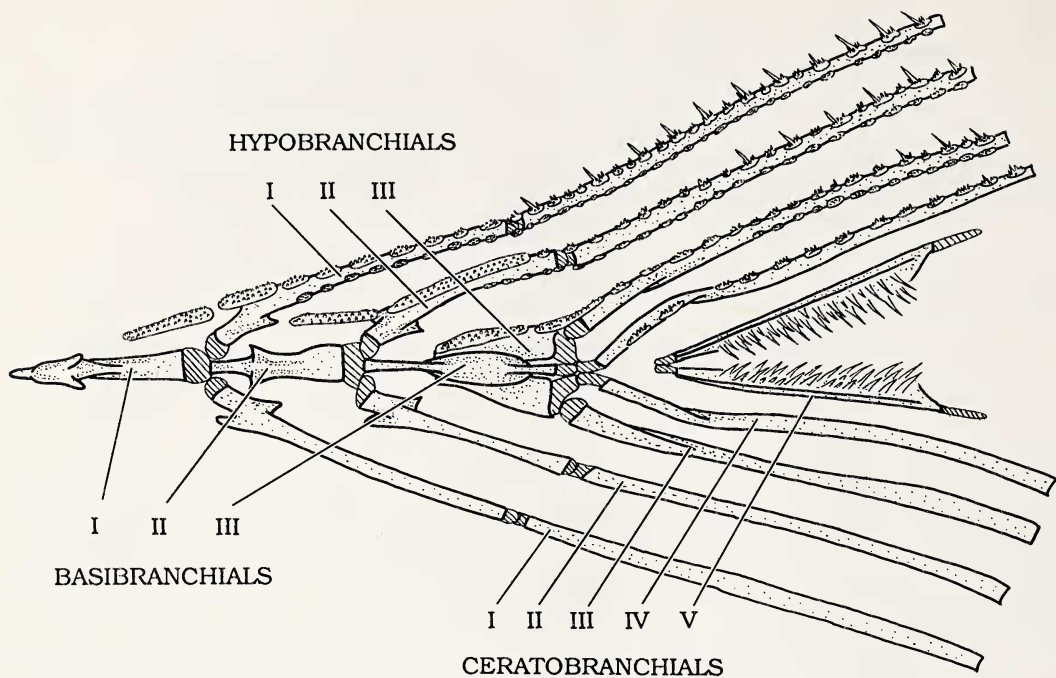
Figure 14. F-K. Lateral view of the left hyoid complex; the glossohyal is represented from left to right in ventral and dorsal views, respectively: (F) *Eupleurogrammus glossodon*; (G) *Evoxymetopon taeniatus*; (H) *Lepidopus fitchi*; (I) *Lep-turacanthus savala*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.

the posteroventral processes are located farther posteriorly and the glossohyal bears a more reduced posterior articular head.

Urohyal

The urohyal is a median bone with an anterior end that is a thin rod bearing a small articular head. This articular head is generally forked and is connected to the ventral hypohyals by two strong lat-

eral ligaments. Posterior to the articular head, the outgroup *Paradiplospinus antarcticus* bears a small posteriorly directed dorsal process (the basibranchial attachment of Kusaka, 1974). This interpretation differs from Russo's (1983: character 54) observations, which indicated that such a dorsal process is absent in all gempylids, except *Epinnula*, *Lepidocybium*, *Thyrsitoides*, and *Thyrsitops*. All trichiurids and the rest of the outgroups in this study lack this dorsal process on the urohyal. Pos-



teriorly, the urohyal is poorly ossified and laterally compressed into a plate-like process that is attached to the cleithrum and coracoid by the sternohyoideus.

Branchiostegal Rays

Seven acinaciform branchiostegal rays (McAllister, 1968) are associated with each side of the hyoid complex. The articular heads are spatulate and expanded to a greater degree in the posterior-most three rays. The three anterior rays are the shortest, and they articulate medially with the ventral margin of the ceratohyal. The fourth branchiostegal ray articulates laterally at the posteroventral corner of the ceratohyal, whereas the three posterior rays articulate laterally with the ventral margin of the epihyal. This distribution of the branchiostegal rays was interpreted by Russo (1983: character 53) as a synapomorphy uniting all gempylids. Johnson (1986: character 10) concluded that the articulation of the fifth branchiostegal on the anteroventral corner of the epihyal represents a synapomorphy for the Scombroidei.

BRANCHIAL COMPLEX

Only the branchial complex of *Trichiurus lepturus* is drawn (Fig. 15) because most of the characters differ only slightly in magnitude and can be easily identified on *Trichiurus*. The first and second basibranchials are also drawn separately for all the genera analyzed, except *Gempylus* and *Nesiarchus* (Fig. 16). Collette et al. (1984: character 1) and Johnson (1986: character 6) indicated that in the scombroids the cartilaginous anterior tip of the second epibranchial articulates with the second pharyngobranchial. A medial cartilaginous process of the second epibranchial extends well beyond the lateral margin of the third pharyngobranchial and articulates with a small cartilaginous condyle at the anterior tip of a longitudinal column that runs along the dorsal surface of the third pharyngobranchial.

Scombroids are also characterized by the absence of the fourth pharyngobranchial cartilage (Johnson, 1986: character 7). The fourth epibranchial articulates with a more extensive posterior cartilage of the third pharyngobranchial. The extensive posterior cartilaginous tip of the third pharyngobranchial fits into the dorsal surface of the fourth pharyngeal tooth plate.

In addition, scombroids are characterized by the presence of fourth pharyngeal tooth plates and by having extremely elongate third pharyngobranchials. The third pharyngobranchial bears a reduced

lateral shelf that has a straight medial margin (Johnson, 1986: character 8).

Lower Branchial Apparatus

BASIBRANCHIALS. The basibranchials are median bones arranged in a longitudinal series. The first basibranchial articulates anteriorly with the posterior margin of the glossohyal and lies between the left and right dorsal hypohyals. The second serves as the point of articulation for the first hypobranchial. In all outgroups and trichiurids, the third basibranchial has a tubular central axis with lateral shelves that cover the medial margins of the third hypobranchial.

Character 17. All of the trichiurids are characterized by the presence of a well-developed, knob-like, anterior articular head on the first basibranchial. In addition, in all trichiurids, except *Aphanopus*, *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus*, the articular head has small dorsolateral processes or wings. All outgroups have a first basibranchial with a broad base that gradually tapers to a point anteriorly.

Character 18. The second basibranchial in the outgroups has an expanded posterior margin and elongate anterior end. Russo (1983: character 62) considered this condition as a synapomorphy uniting the gempylids *Diplospinus*, *Gempylus*, *Nesiarchus*, and *Paradiplospinus*. In the trichiurids, the second basibranchial bears two small, laterally pointed processes posterior to the place of articulation with the heads of the first hypobranchial.

HYPOBRANCHIALS. The hypobranchials are three pairs of bones that form part of the lower arms of the gill arches; their dorsal heads articulate with the ceratobranchials. The ventral heads of the first and second hypobranchials articulate with the cartilaginous junction between the first and second and second and third basibranchials, respectively. The third hypobranchial is triangular and smaller than the first and second hypobranchials, and it has an elongate anterior process that extends under the lateral shelves of the third basibranchial.

The first hypobranchial has a medially curved articular head that may bear a lateral or a medial process, or both. Russo (1983: character 63) noted the absence of an anterior (lateral) process in the first hypobranchial of all gempylids, except *Diplospinus*, *Gempylus*, *Lepidocybium*, and *Tongaichthys*. He considered the presence of an anterolateral process to be plesiomorphic. All trichiurids, except *Aphanopus* and *Benthodesmus*, and outgroups, except *Nesiarchus*, have a medial and a lateral process on the anterior articular head of the first hypobranchial. The cleared and stained specimens of

Figure 15. Dorsal view of the lower branchial apparatus of *Trichiurus lepturus* (top), the left side does not include the gill rakers or tooth patches; cartilaginous articulations striped. Right upper branchial apparatus of *Trichiurus lepturus*: ventral view (center); dorsal view showing the cartilaginous articulations (bottom).

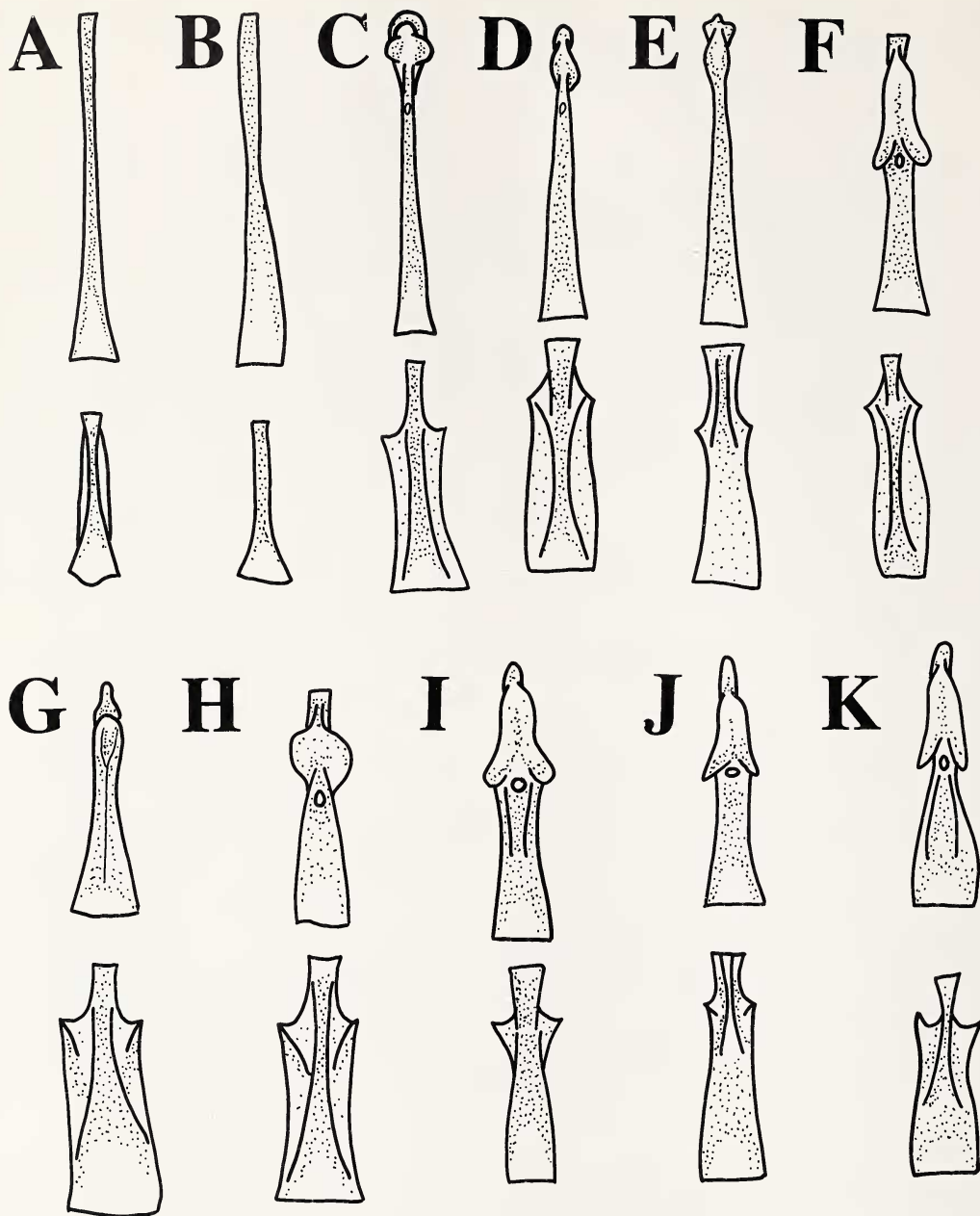


Figure 16. Dorsal views of the first basibranchial (top) and second basibranchial (bottom) of: (A) *Diplospinus multistriatus*; (B) *Paradiplospinus antarcticus*; (C) *Aphanopus arigato*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*; (F) *Eupleurogrammus glossodon*; (G) *Evoxymetopon taeniatus*; (H) *Lepidopus fitchi*; (I) *Lepturacanthus savala*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.

Benthodesmus tenuis and *Nesiarchus* analyzed in this study lacked both lateral and medial processes on the first hypobranchial. The specimens of *Aphanopus* and *B. simonyi*, however, had only well-developed medial processes. The medial and lateral processes are well developed in the rest of the trichiurids analyzed, where they clearly extend far from the lateral and medial margins of the first

hypobranchial. *Diplospinus* and *Paradiplospinus* also bear well-developed medial processes on the first hypobranchial, but their lateral processes are reduced and appear as rounded outgrowths that may extend only slightly past the margin of the first hypobranchial. This condition differs from the observations of Russo (1983) who noted that, whereas *Diplospinus* bears a lateral process on the first

hypobranchial, *Paradiplospinus* lacks such a structure.

The second hypobranchial has a slightly curved articular head and bears no distinct lateral or medial processes in the outgroups, except *Gempylus*, which seems to bear a reduced lateral process on the second hypobranchial. All trichiurids are characterized by the presence of distinct lateral and medial processes in the second hypobranchial. These processes are usually pointed and well defined, except in *Aphanopus* and *Benthodesmus* where they may be reduced. The specimens of *Benthodesmus tenuis* have reduced medial and lateral processes, whereas those of *B. simonyi* have well-developed medial processes. The presence or absence of lateral and medial processes in the first and second hypobranchials is quite variable among and within genera, and its categorization into objective character states is difficult.

The third hypobranchial is triangular, with the tubular anterior end curving medially under the lateral wings of the third basibranchial. In all trichiurids and outgroups, except *Aphanopus*, *Benthodesmus*, *Gempylus*, and *Nesiarchus*, the posterolateral corner of this bone usually bears pointed projections. This condition varies between specimens of the same species, and it is dependent on the size of the specimens available and the degree of ossification of this bone in any given specimen. In some species, the posteromedial corners of this paired bone cover the posterior end of the third basibranchial.

CERATOBANCHIALS. The ceratobranchials are pairs of bones that form the lower arms of the gill arches. These are the longest bones in the gill arches, and they support most of the gill filaments and rakers. The anteroventral heads of the first, second, and third ceratobranchials articulate with the first, second, and third hypobranchials, respectively. The anteroventral head of the fourth ceratobranchial articulates with the third basibranchial. The posterior tip of the fifth ceratobranchial has an elongate cartilaginous cap that lies within the epithelium of the branchial cavity. The anterior cartilaginous tips of the paired elements of the fifth ceratobranchial may be fused at their tips and articulate with the complex of the fourth ceratobranchial and third basibranchial by ligaments. The fifth ceratobranchial bears dorsal tooth plates. The morphology of the fifth ceratobranchial is similar among the taxa analyzed in this study.

Character 19. The outgroups and trichiurids have straight first, second, and third ceratobranchials. Russo (1983: character 64) considered the sigmoid shape of the fourth ceratobranchial to be a synapomorphy uniting the gempylids *Diplospinus* and *Paradiplospinus*. In the trichiurids and the rest of the outgroups and gempylids, the anteroventral head of the fourth ceratobranchial is twisted medially, but the bone does not appear sigmoidal. Although this character appears equivocal at the out-

group node, I agree with Russo (1983) and consider the presence of a sigmoidal fourth ceratobranchial as a synapomorphy uniting *Diplospinus* and *Paradiplospinus*.

Upper Branchial Apparatus

EPIBRANCHIALS. The epibranchials are four pairs of bones that form part of the upper arms of the gill arches. The posteroventral ends of the epibranchials articulate with the posterodorsal ends of the ceratobranchials. The anterodorsal head of the first epibranchial articulates with the first pharyngobranchial and bears an uncinate process that articulates with the second pharyngobranchial by way of an interarcual cartilage. The anterodorsal head of the second epibranchial articulates not only with the second pharyngobranchial but also with the third pharyngobranchial via an elongate medial cartilaginous process. This medially elongate cartilaginous process joins a small articular condyle on a longitudinal ridge of the dorsal face of the third pharyngobranchial. Posterior to this cartilaginous head, all gempylids and trichiurids, except *Lepturacanthus* and *Trichiurus*, have a truncated dorsomedial process that bears a ligamentous attachment to the third epibranchial. *Lepturacanthus* and some specimens of *Trichiurus* are characterized by having a second epibranchial in which the dorsomedial process is pointed. The third epibranchial also bears a dorsomedial process that connects it to the fourth epibranchial and a cartilaginous knob at the anterior tip that attaches it to the third pharyngobranchial. In *Diplospinus* and *Paradiplospinus*, a shelf-like dorsomedial plate extends longitudinally between the anterodorsal process and the posterior end of the third epibranchial. The rest of the outgroups and the trichiurids lack such a modification or have a partial shelf that does not extend along the entire posterior half of the third epibranchial. However, the extent of this shelf is variable and difficult to categorize into well-defined character states. A dorsolateral process on the fourth epibranchial articulates with the third epibranchial.

PHARYNGOBRANCHIALS. The pharyngobranchials are three pairs of small bones that are attached to the anterodorsal heads of the epibranchials. The first pharyngobranchial articulates dorsally with the prootic. In all trichiurids and outgroups, the first pharyngobranchial is a small, tubular, edentulous bone. In *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*, the first pharyngobranchial is strongly curved, whereas in the rest of the trichiurids and the outgroups, the bone is straight or slightly curved. The degree of curvature on the first pharyngobranchial is highly variable and difficult to categorize.

The second and third pharyngobranchials bear well-developed tooth plates ventrally. The third pharyngobranchial is the largest, and it bears a small dorsolateral cartilaginous knob that articulates with the cartilaginous tip of the second epi-

branchial. The posterior margin of the third pharyngobranchial bears a large cartilaginous cap that articulates with the third and fourth epibranchials.

GILL RAKERS. Gill rakers tend to be more reduced and poorly ossified in the outgroups *Diplospinus*, *Nesiarchus*, and *Paradiplospinus*. The better ossified gill rakers of the trichiurids can be spinous, tuberculous, or a combination of both, with the spinous ones usually at the posterior end of the hypobranchials. Trichiurids have two rows (lateral and medial) of gill rakers on the first and second hypobranchials, except *Benthodesmus*, which bears a single row on the first hypobranchial. All outgroups have a single row of gill rakers on the first hypobranchial and two rows on the second hypobranchial, except *Gempylus*, which has single rows on the first and second hypobranchials. In all trichiurids and outgroups, except *Nesiarchus*, the lateral rows of gill rakers on the first and second hypobranchials extend anteriorly past the articular head of the bone as part of the epithelial covering of the branchial arches. The third hypobranchials bear small tuberculous gill rakers, which are extremely reduced in *Diplospinus* and *Paradiplospinus*.

The outgroups and trichiurids have first, second, and third ceratobranchials bearing two longitudinal (lateral and medial) series of gill rakers on the anterior margins. The lateral series of gill rakers are spinescent, with spine length increasing toward the posterodorsal end where these bones articulate with the epibranchials. The medial series of gill rakers tend to be smaller and more tuberculous in nature. The fourth ceratobranchial may bear one or two rows of gill rakers. The medial row is present only in the largest specimens, and it is extremely reduced and nonspinous.

All the epibranchials in most of the taxa analyzed have either one or two series of gill rakers or tooth plates along their ventral margin. In *Diplospinus*, *Nesiarchus*, and *Paradiplospinus*, the fourth epibranchial is edentulous. The size and number of gill rakers and tooth plates on the other epibranchial bones are reduced in the outgroups *Diplospinus* and *Paradiplospinus*. The trichiurids and the rest of the outgroups have epibranchials bearing gill rakers or tooth plates with stronger spination.

All trichiurids and *Gempylus* have two ventral series of gill rakers on the third epibranchial. In *Diplospinus*, *Nesiarchus*, and *Paradiplospinus*, there is only a single series of reduced gill rakers on this bone. Russo (1983: character 65) indicated that all gempylids have two rows of tooth plates on the third epibranchial, except *Epimmula*, *Paradiplospinus*, and *Thyrsitops*, which bear one row, and *Ruvettus* and *Thyrsites*, which bear no rows. The observation of a single row of gill rakers on the third epibranchial of *Diplospinus* differs from the condition noted by Russo (1983). However, the presence or absence of gill rakers on these bones is difficult to evaluate since the gill rakers are ex-

tremely reduced and could easily be lost during handling and dissection.

Matsubara and Iwai (1958) noted that *Gempylus* differs from other gempylid genera in that the gill raker at the angle of the first gill arch is small, triangular, and exposed at its tip. The rest of the gempylids have a gill raker at the angle of the arch that is T-shaped, larger, and more exposed. In the diagrams of Nakamura and Parin (1993: figs. 26, 27), it is evident that some trichiurids share, with *Gempylus* and *Paradiplospinus*, the presence of a small gill raker at the angle of the first gill arch. The gill raker at the angle between the first ceratobranchial and the first epibranchial in *Aphanopus*, *Assurger*, and *Benthodesmus* has a longer spine with an expanded tip. Tucker (1956) described the morphology of the gill rakers in *Benthodesmus tenuis*, noting that some of the gill rakers toward the angle of the gill arches have one large barbed spine. However, the size and shape of the spines on the gill rakers is quite variable between specimens. The gill raker at the angle between the first epibranchial and first ceratobranchial in *Diplospinus* and *Paradiplospinus* is characterized by having a base that bears a small root-like process extending toward the articulation of the ceratobranchial and epibranchial bones. In *Nesiarchus*, the tips of the base in this gill raker bend toward the first epibranchial-first ceratobranchial junction, giving it the appearance of a tri-rooted element. *Gempylus* is characterized by having an angular gill raker with a triangular base that lacks these root-like processes. The angular gill raker in the trichiurids has a circular base bearing one larger spine surrounded by smaller spinules, and it lacks the root-like process observed in *Diplospinus* and *Paradiplospinus*. Although the difference in morphology of the angular gill raker between the trichiurids and the outgroups is obvious, the condition at the outgroup node appears equivocal, and the character is uninformative within the trichiurids. Thus, the morphological features of the angular gill rakers are excluded from this analysis, but they remain as a potentially informative character, or characters, for a future study in which both the trichiurids and gempylids are analyzed together.

NEUROCRANIUM

In dorsal view, the neurocranium of the trichiurids and outgroups is triangular, being narrow anteriorly and wider posteriorly (Fig. 17). The skulls of most gempylids and all trichiurids are mainly characterized by the elongation of some of their bones. Posterodorsally, the neurocranium bears three prominent ridges. Medially, a single supraoccipital ridge is formed by the confluence of two frontal ridges onto the supraoccipital. Lateral to the supraoccipital ridge, a pair of epiotic ridges extends through the parietal and the posterior edge of the frontal. Lateral to the epiotic ridge, a pair of pter-

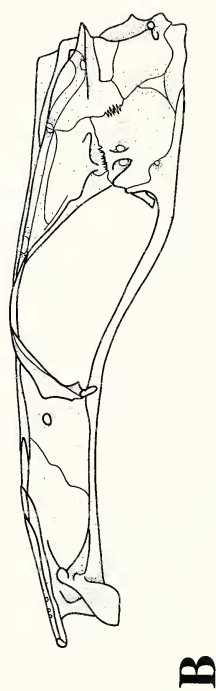
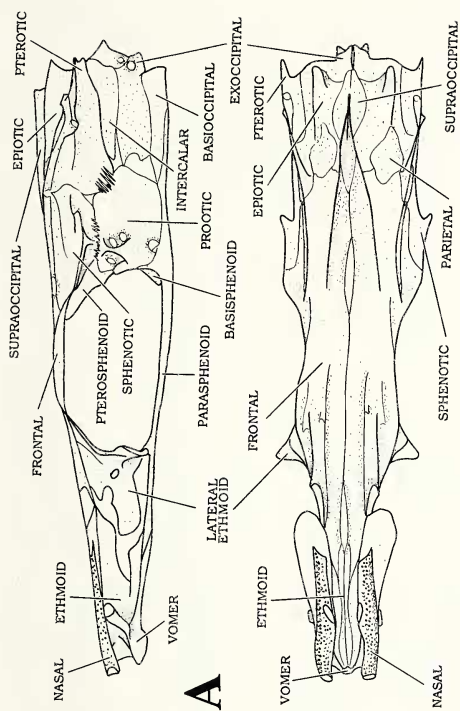


Figure 17. A-B. Lateral and dorsal views (top and bottom, respectively) of the neurocranium: (A) *Diplospinus multistriatus*; (B) *Paradiplospinus antarcticus*.

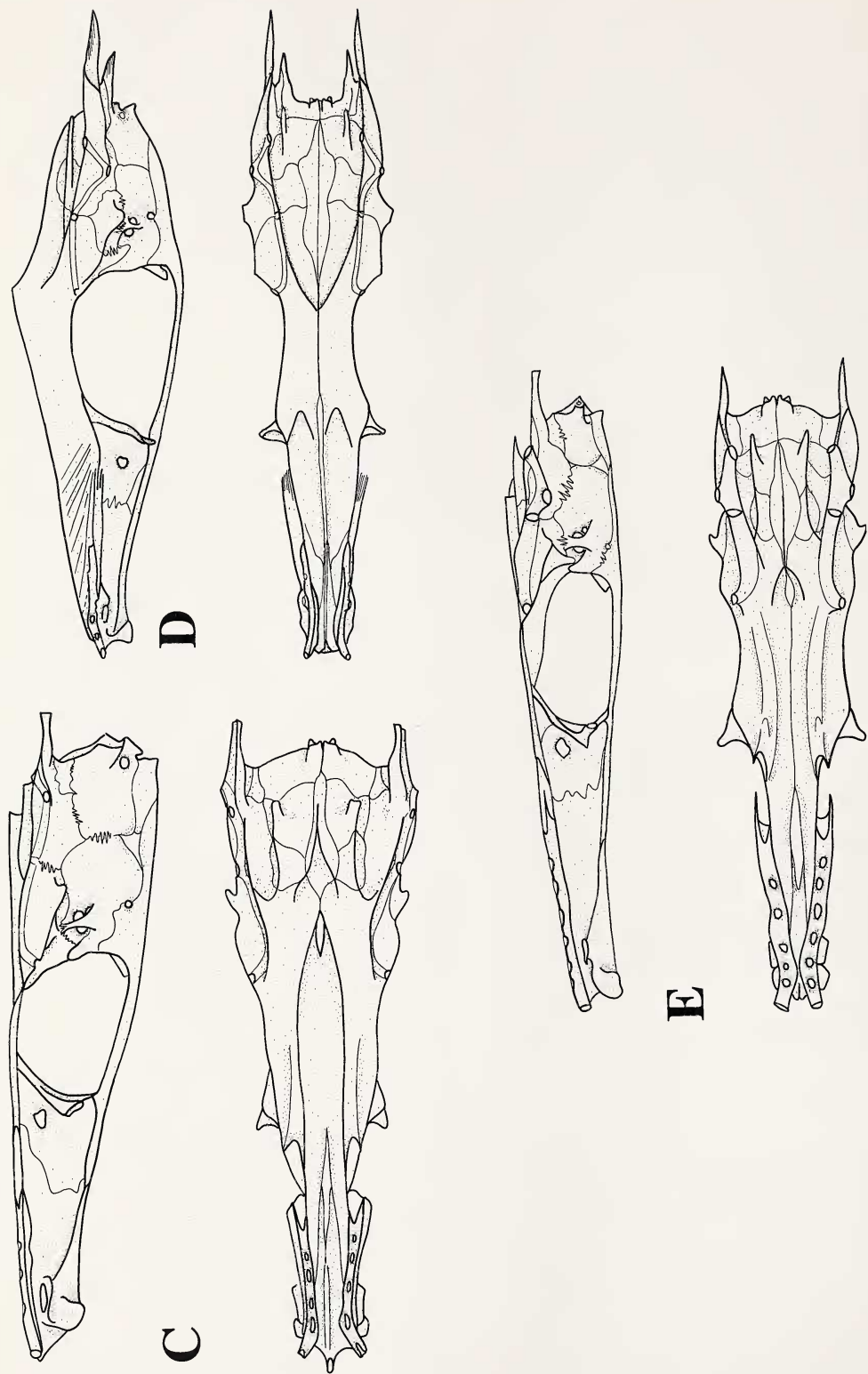


Figure 17. C-E. Lateral and dorsal views (top and bottom, respectively) of the neurocranium: (C) *Aphanopus arigato*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*.

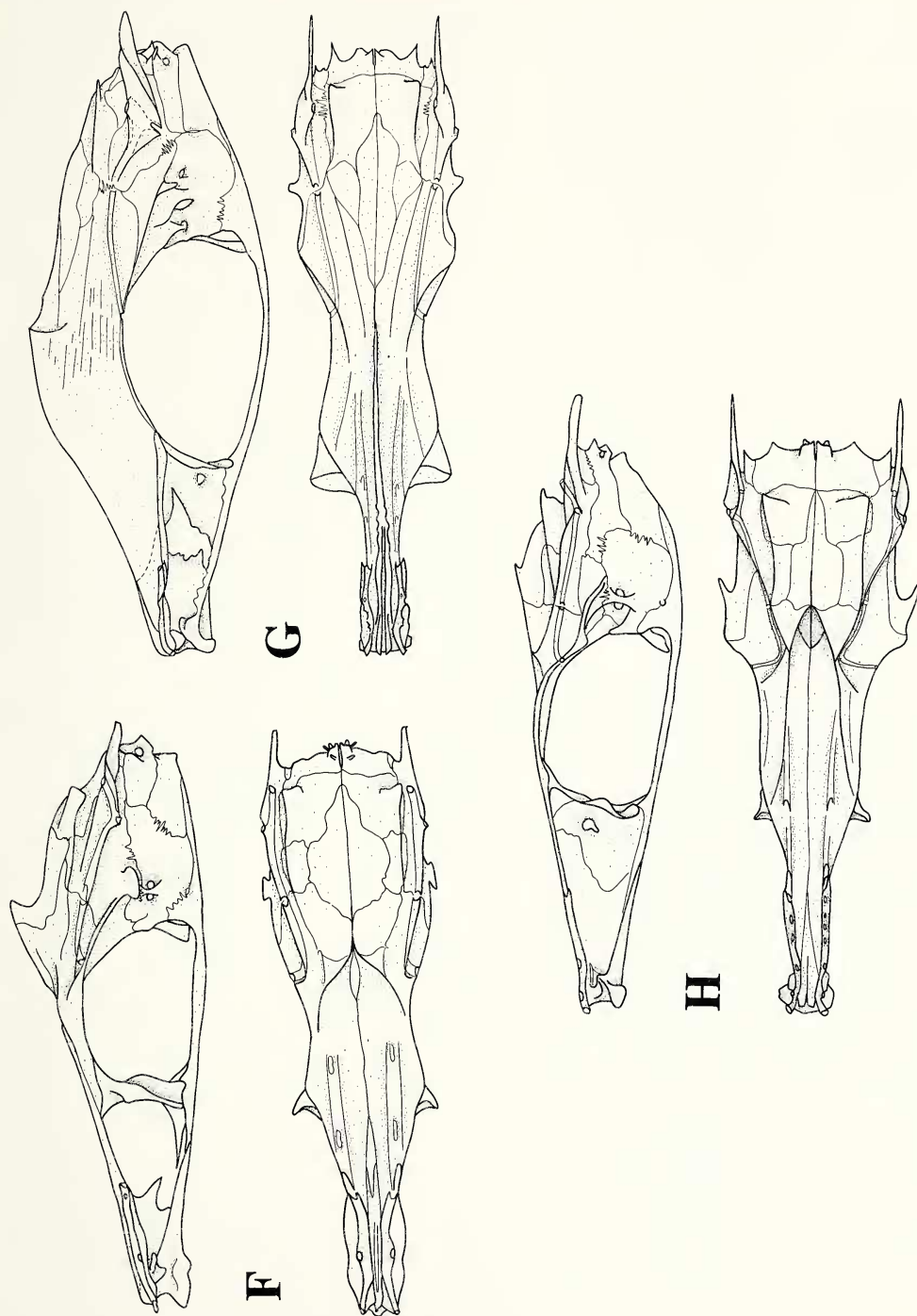


Figure 17. F-H. Lateral and dorsal views (top and bottom, respectively) of the neurocranium: (F) *Eupleurogrammus glossodon*; (G) *Eroxymetopon taeniatus*; (H) *Lepidopus fitchi*.

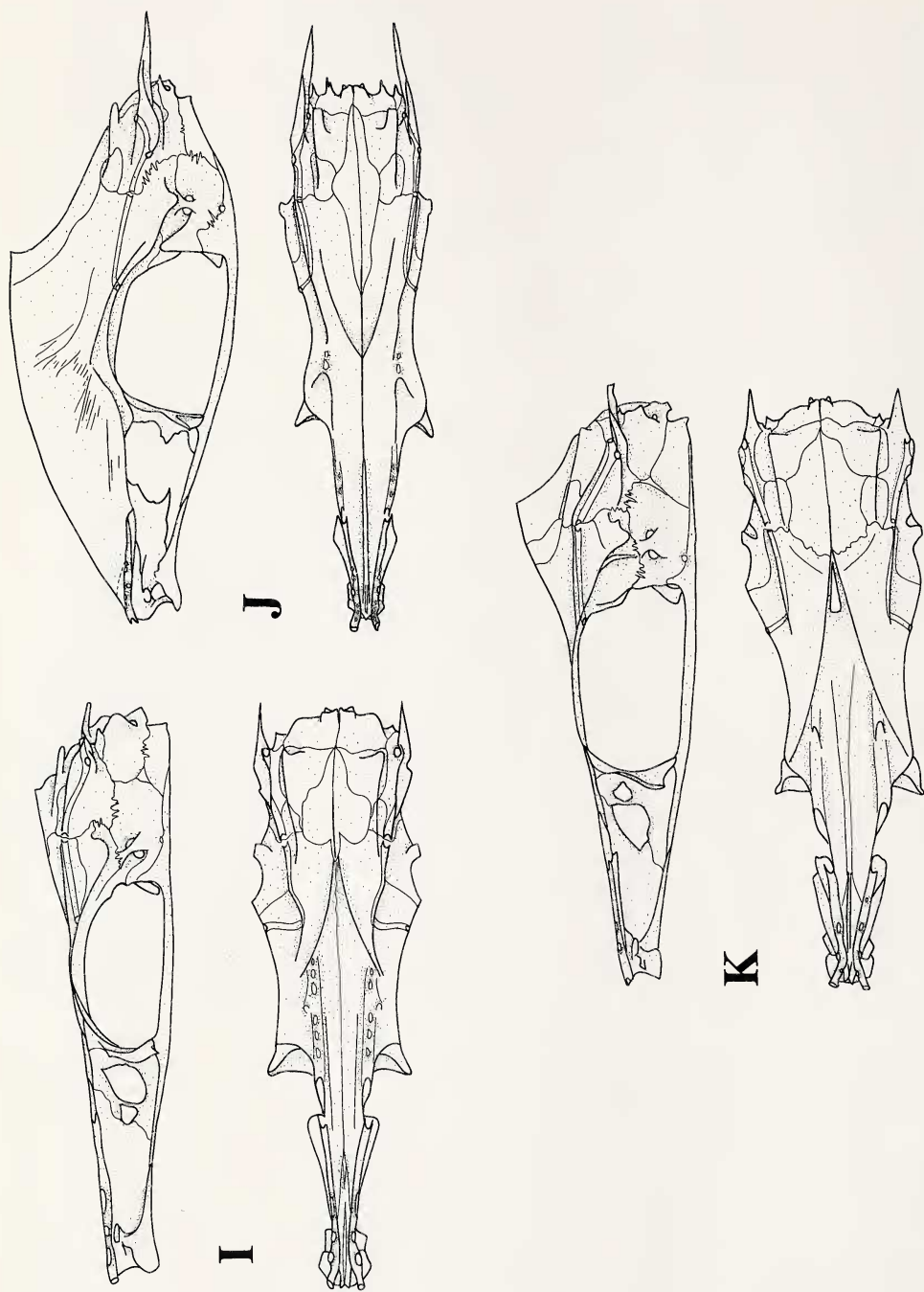


Figure 17. I-K. Lateral and dorsal views (top and bottom, respectively) of the neurocranium: (I) *Lepturacanthus savala*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.

otic ridges extends through the pterotic and the frontal.

Ethmoidal Region

NASAL. The nasal appears as a simple tube in the outgroup *Nesiarchus* and the trichiurids *Benthodesmus* and *Lepidopus*. Ossified, lateral laminar extensions are present on the nasal and cover the lateral palatal processes of the ethmoid in the outgroups *Gempylus* and *Paradiplospinus* and the trichiurids *Assurger* and *Eupleurogrammus*. The rest of the trichiurids and outgroups bear laminar extensions that do not cover the palatal processes of the ethmoid. *Eupleurogrammus*, *Evoxymetopon*, *Gempylus*, and *Paradiplospinus* are characterized by lateral laminar extensions that extend along the whole length of the nasal. In addition, *Eupleurogrammus* bears smaller medial extensions anteriorly. The lateral extensions are restricted to the posterior half of the nasal in the outgroup *Diplospinus* and the trichiurids *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*. This potential character is difficult to evaluate because the detection of such lateral extensions depends on the degree of ossification of the lateral membrane on the nasal. For example, whereas some specimens of *Diplospinus*, *Lepidopus*, and *Paradiplospinus* seem to show the presence of well-developed, ossified lateral extensions, others are characterized by their reduction or absence.

Character 20. The nasal is straight and runs parallel to the ethmoid and frontal in the outgroups. The anterior head of the nasal is curved laterally in all the trichiurids. The anterior head of the nasal in one of the specimens of *Nesiarchus* appeared to be slightly curved, but the condition is not comparable to that of the trichiurids, in which the anterolateral margin of the nasal appears concave in dorsal view and clearly extends past the lateral margin of the ethmoid.

ETHMOID. Anterodorsally, the ethmoid supports the nasal and bears two lateral processes, that are attached to the palatine (the palatal processes of Russo, 1983). Anteroventrally, the ethmoid articulates with the dorsal edge of the vomer. Posteriorly, it abuts the lateral ethmoid and articulates with the anterior margin of the frontal. The ethmoid is elongate in all trichiurids and the outgroups.

Character 21. In *Assurger*, *Evoxymetopon*, *Lepidopus altifrons*, and *Tentoriceps*, the ethmoid bears two dorsally expanded ridges that extend well above the dorsal margin of the nasal in lateral view. The dorsal ridges on the ethmoid of *Evoxymetopon* and *Tentoriceps* are more elevated and appear triangular in lateral view. *Aphanopus*, *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* are characterized by the presence of two longitudinal ridges on the dorsal face of the ethmoid. However, these ridges do not extend well above the nasal in lateral view. Russo (1983: character 2) not-

ed that the presence of a medial ridge on the dorsal surface of the ethmoid represented a synapomorphy uniting the gempylid genera *Diplospinus* and *Paradiplospinus*. This ridge is reduced and does not extend well above the nasal. The other outgroups in this study, plus *Benthodesmus*, *Lepidopus caudatus*, and *L. fitchi*, lack a dorsal ridge on the ethmoid.

LATERAL ETHMOID. Anteriorly, the lateral ethmoid joins the vomer and the ethmoid. It attaches to the frontal dorsally and the parasphenoid ventrally. The posterior margin of the lateral ethmoid forms a lateral process that is divided into a ventral and a dorsal articular head. The ventral articular head attaches to the palatine, whereas the dorsal articular head joins the dorsal articular process of the lachrymal.

The articulations of the lachrymal and palatine with the ethmoid are by way of cartilaginous knobs that may or may not be separated by a bony ridge. Russo (1983: character 8) considered the absence of a bony ridge as the apomorphic condition among some of the gempylids in his study. All of the outgroups and the trichiurids share this derived condition.

VOMER. The vomer articulates anterodorsally with the ethmoid and posteriorly with the lateral ethmoid and the parasphenoid. The trichiurids and all outgroups have a vomer with an expanded anteroventral head that lacks teeth. In all trichiurids, except *Assurger* and *Eupleurogrammus*, the anterior margin of the head of the vomer appears flat in ventral view. *Eupleurogrammus* and *Gempylus* are similar in that the anterior margin of the ventral head bears an anteriorly elongate process. *Assurger* and *Paradiplospinus* tend to have a rounded anterior margin on the head of the vomer, whereas *Nesiarchus* and some specimens of *Diplospinus* bear a flat anterior margin. However, the condition seems variable within species. For example, Russo (1983: character 10) noted that the anterior margin of the vomer in the gempylids *Diplospinus*, *Gempylus*, *Neoepinnula*, *Nesiarchus*, *Paradiplospinus*, *Ruvetus*, *Thyrsites*, and *Thyrsitops* is rounded in ventral view. In this study, however, one specimen of *Diplospinus multistriatus* has a rounded head on the vomer; another has a flat anterior margin.

Anteriorly, the vomer has a process that extends anterodorsally and attaches to the anterior tip of the ethmoid. All the trichiurids and the outgroups, except *Aphanopus*, have a vomer in which the anterior tip of this process terminates below or slightly anterior to the ethmoid. In *Aphanopus*, this process is extremely elongate and extends slightly past the anterior margin of the rostral cartilage.

Orbital Region

FRONTAL. Anteriorly, the frontal attaches to the nasal, ethmoid, and lateral ethmoid. Posteriorly, it articulates with the pterospheonoid, sphenotic, parietal, and supraoccipital. Medially, the frontals are

joined to each other. A pineal foramen appears as a gap in this medial junction and is located anterior to the supraoccipital. The pineal foramen is not evident in some large specimens and those trichiurids with a well-developed frontal crest. Russo (1983) noted that there are variations in the size of the pineal foramen among gempylids and indicated that in some genera, such as his outgroup *Pomatomus* Lacepède 1802, the pineal foramen is not present because the supraoccipital crest is carried forward as a ridge onto the frontal. Ventrally, there are short, poorly developed sheets of bone (the orbital lamellae of Collette and Russo, 1984) that abut the lateral ethmoid anteriorly and the pterosphenoid posteriorly. Anterolaterally, the frontal carries the supraorbital canal of the laterosensory canal system, and posterolaterally it carries the anterior half of the otic canal (Coombs et al., 1987). Johnson (1986: character 3') noted that, in the scombroids, the frontosphenotic shelf is horizontal and has a sharp edge. The supraorbital canal is separated from the dorsolateral margin of the orbit by a large fossa that houses the dilatator operculi. The infraorbital canal passes over the sharp edge of the frontosphenotic shelf and joins the supraorbital canal medially.

Character 22. Johnson (1986: character 29) noted that in the trichiurids the supra- and infraorbital canals are joined by way of a bony tube that extends laterally from the supraorbital canal. This condition is present in all the trichiurids studied. The plesiomorphic condition observed in all other scombroids is characterized by the presence of an elongate dilatator operculi fossa that separates the junction of the infra- and supraorbital canals, which communicate through a dorsally or laterally directed pore on the frontal ridge (Johnson, 1986).

Character 23. Two frontal ridges become confluent posteriorly, forming the supraoccipital ridge. In *Assurger*, *Evoxymetopon*, and *Tentoriceps*, the frontal ridges become confluent well anterior to the supraoccipital (on the ethmoidal region) and form an extremely well-developed frontal crest that appears as laterally flat sheets. *Lepidopus altifrons* is unique among the species of this genus in having a well-developed frontal that is similar to that of *Assurger*, *Evoxymetopon*, and *Tentoriceps*. Tucker (1957: 426), in his description of a specimen of *Evoxymetopon taeniatus* (= *L. altifrons*), noted that the ridge-like elevation of the ethmofrontal region "is not so much an osseous elevation but an outgrowth of soft tissue, normally increasing with age as in numerous other percomorph fishes." The frontal crest present in the ethmofrontal region of *Assurger*, *Evoxymetopon*, *Lepidopus altifrons*, and *Tentoriceps* is flexible, but it represents an ossified extension of the frontal ridges. In *Eupleurogrammus*, the frontal ridges become confluent anterior to the supraoccipital and form a frontal crest that is elevated above the interorbital space. These ridges in *Eupleurogrammus* are laterally convex. In the rest of the trichiurids and the outgroups, the frontal

ridges are not elevated as a frontal crest, and they do not become confluent until they reach or are close to the supraoccipital.

The frontal crest in *Assurger*, *Evoxymetopon*, *Lepidopus altifrons*, and *Tentoriceps* extends above the orbits making the interorbital space convex. *Lepidopus dubius* Parin and Mikhailin 1981 is the only species within the genus that is similar to *L. altifrons* in the morphology of the frontal region. However, in *L. dubius*, the frontal ridges are not as elevated as in *L. altifrons*, do not extend far onto the ethmoidal region, and become confluent closer to the posterior margin of the orbits. The rest of the trichiurids and the outgroups have an interorbital space that is concave or flattened. Parin and Collette (1993) warned that the presence of a convex interorbital space and a sagittal crest that extends onto the ethmoidal region are characters that seem to change in a gradual manner in the series *L. manis* Rosenblatt and Wilson 1987 and *L. fitchi*, *L. caudatus*, and *L. calcar* Parin and Mikhailin 1982, *L. dubius*, and *L. altifrons*. *Assurger*, *Evoxymetopon*, and *Tentoriceps* could be added to this series as a more derived condition.

PTEROSPHEOID. The pterosphenoid forms the margins of the pterosphenotic window (Collette and Chao, 1975). The pterosphenoid articulates with the frontal dorsally and the basisphenoid ventrally. Ventrolaterally it joins the sphenotic and the prootic. The morphology of this bone is similar among the taxa analyzed in this study.

BASISPHEOID. The basisphenoid is a Y-shaped median bone. The elongate ventral process, or base, of the basisphenoid extends toward the parasphenoid and bisects the entrance of the posterior myodome (Russo, 1983). Dorsally, it joins the posteroventral edges of the pterosphenoid, whereas laterally it attaches to the prootic. The morphology of this bone is similar among the taxa analyzed in this study.

SCLEROTICS. The sclerotics are ossifications of the cartilaginous or fibrous regions on the sclera of the eyes. Nakamura and Yamaguchi (1991) found that the 21 teleost species analyzed in their study had at most two sclerotics occupying the anterior and posterior poles of the scleral equator.

Character 24. No ossified sclerotics are present in the trichiurids and the outgroups *Diplospinus* and *Paradiplospinus*. However, the outgroups *Nesiarchus* and *Gempylus* have anterior and posterior sclerotics on the scleral equator. I have found no information in the literature about the presence of these ossifications among the rest of the gempylids. Nakamura and Yamaguchi (1991) included two scombroids in their analysis: *Thunnus thynnus* (Linnaeus 1758) and *Trichiurus lepturus*. They indicated that *Thunnus thynnus* has sclerotics that grow to form a complete ring around the sclera, whereas *Trichiurus lepturus* lacked paired sclerotics. Although they did not consider them scombroids, Nakamura and Yamaguchi (1991) also described the sclerotics of a marlin and a barracuda.

They noted that both of these species have a pair of sclerotics. Collette and Chao (1975) described the presence of sclerotics in all the genera of the tribe Sardini within the family Scombridae. Furthermore, Collette and Russo (1984) also noted the presence of sclerotic bones in the genera *Acanthocybium* Gill 1862, *Grammatorcynus*, and *Scomberomorus*. Although the character is variable within the outgroups, I consider the absence of sclerotics as the apomorphic condition since the presence of these ossifications seems to be widely distributed among the scombroids. The presence of sclerotics in the sphyræniids might be a good indicator of the plesiomorphic state of this condition because the barracudas have been proposed as the sister group to the rest of the scombroids (Collette and Russo, 1986; Johnson, 1986; Carpenter et al., 1995).

Otic Region

SUPRAOCCIPITAL. The supraoccipital is a median bone forming the posterodorsal corner of the neurocranium. A supraoccipital crest, which originates posterior to the pineal foramen, is formed by the confluence of two ridges from the frontal. The supraoccipital articulates anteriorly with the frontal, posteriorly with the exoccipital, and laterally with the parietal and the epiotic.

Starks (1911) described a specimen of *Trichiurus lepturus* in which the epiotic, frontal, parietal, and supraoccipital were covered by a spongy, bony substance. James (1960) and Nakamura and Parin (1993) reported that some specimens of *T. lepturus* from waters around India show extreme ossification (hyperostosis of Barnard, 1948) of the supraoccipital bone. James (1960) indicated that, in those specimens of *T. lepturus* with extreme hyperostosis of the supraoccipital, the whole occipital region of the neurocranium may be covered by a thickened bony mass, which may extend to the first or second vertebral elements. He remarked that in those specimens the preoccipital profile of the head approaches the orbital region steeply. Some of the specimens of *T. lepturus* analyzed in this study also show the presence of hyperostosis on the supraoccipital. No instances of hyperostosis on the supraoccipital have been noted in any other trichiurid or gempylid. Smith-Vaniz et al. (1995) listed the presence of hyperostotic bones on 92 species belonging to 22 teleost families and concluded that hyperostosis has arisen independently many times among the teleosts.

Character 25. Russo (1983: character 20) noted that the supraoccipital of *Diplospinus*, *Nealotus*, *Nesiarchus*, and *Paradiplospinus* is a small thin ridge, low on the cranium. He noted that all the other gempylids in his study, except *Lepidocybium* and *Ruvettus*, have a moderately high supraoccipital crest, extending well above the epiotic ridges. Russo (1983) described the supraoccipital crest of *Gempylus* as being moderate to low in height. In contrast to Russo's (1983) observation, the speci-

men of *Gempylus* analyzed in this study has a supraoccipital crest that is higher than in the other outgroups, but it runs parallel to the epiotic ridges. The other outgroups, plus the trichiurids *Aphanopus* and *Benthodesmus*, are characterized by having a supraoccipital crest that is reduced and runs close and nearly parallel to the epiotic ridges. In lateral view, the rest of the trichiurids have a higher supraoccipital crest that does not run parallel to the epiotic ridges and that extends posterodorsally, diverging at an angle from the epiotic ridges. Thus, the outgroups and the trichiurids *Aphanopus* and *Benthodesmus* have a neurocranium with a dorsal profile that appears flat in lateral view.

Character 26. In Assurger, *Evioxymetopon*, *Lepidopus altifrons*, and *Tentoriceps*, the highest point of the supraoccipital crest ends above the orbits. In all other trichiurid and outgroup genera, the highest point of the supraoccipital crest ends posterior to the orbits and above the otic or occipital regions of the neurocranium.

PARIETAL. The parietal articulates with the frontal anteriorly and the epiotic posteriorly. Laterally, the parietal joins the pterotic bone. A ridge that originates on the frontal, lateral to the supraoccipital ridge, continues across the parietal and onto the epiotic. The morphology of this bone is similar among the taxa analyzed in this study.

EPIOTIC. The epiotic articulates anteriorly with the parietal and posteroventrally with the exoccipital. It joins the pterotic laterally and the supraoccipital medially. The epiotic is the posterior-most bone forming the epiotic ridges, which also cross the parietal and extend onto the frontal in the outgroups and most trichiurids. In the trichiurids, the epiotic ridges usually become confluent with the pterotic ridges above the parietal or slightly anterior to it on the frontal. The epiotic serves as the site of attachment for the dorsal articular process of the posttemporal, uniting the neurocranium and the pectoral girdle. The posterior margin of the epiotic appears more pointed and posteriorly elongate in dorsal view in Assurger, *Benthodesmus*, *Gempylus*, and *Nesiarchus* and some specimens of *Diplospinus*, *Lepidopus*, and *Trichiurus*. In contrast, the posterior margin of the epiotic does not become extremely elongate posteriorly and appears to be flat or rounded in the rest of the outgroups and trichiurids. However, the shape of the epiotics is quite variable among and within species. The conditions described above are difficult to categorize objectively and are dependent on the size of the specimens available.

PTEROTIC. The pterotic articulates anteriorly with the frontal and the sphenotic and posteriorly with the exoccipital and the intercalar. It articulates ventrally with the prootic and intercalar and medially with the epiotic and the parietal. Ventrolaterally, the pterotic forms a fossa that serves as the articular facet for the dorsal articular condyle of the hyomandibula. Another fossa at its junction with the sphenotic accepts part of the anterior articular

condyle of the hyomandibula. The posterior portion of the otic branch of the laterosensory canal system (Coombs et al., 1987), the pterotic canal, crosses the pterotic longitudinally. Russo (1983) identified the complete enclosure of the canal as a synapomorphy of the gempylids. The same condition characterizes the trichiurids, although the canal tends to be wider and less ossified in *Aphanopus* and *Benthodesmus*.

Posteriorly, the pterotic bears two pores of the laterosensory canal system. The dorsal pore receives the postotic canal from the anteroventral branch of the supratemporal, and the lateral pore connects to the preopercular canal on the preopercle (Coombs et al., 1987). Russo (1983: character 23) noted that in all gempylids, except *Diplospinus*, *Lepidocybium*, *Nesiarchus*, *Paradiplospinus*, and *Thyrsoitoides*, the dorsal pore extends as a separate canal in a bony shelf away from the main pterotic canal. In *Gempylus*, this shelf appears as a dorsal ridge that runs throughout the whole length of the pterotic canal and completely separates the dorsal and lateral pores. In *Aphanopus*, *Benthodesmus*, and the outgroups, except *Gempylus*, the dorsal pore originates directly from the main pterotic canal, and the dorsal ridge separating the dorsal and lateral pores is extremely reduced or absent. In the rest of the trichiurids, the dorsal pore also originates directly from the main pterotic canal, but the dorsal ridge separating the dorsal and lateral pores is restricted to the posterior portion of the pterotic canal. *Assurger*, *Eupleurogrammus*, *Evoxymetopon*, *Lepidopus*, and *Tentoriceps* bear a well-developed, laterally flattened, porous wall separating the dorsal and lateral pores. However, the extent of the dorsal ridge, as well as the presence of a small porous wall separating the dorsal and lateral pores, is quite variable and difficult to categorize objectively. This potential character is not included in this analysis and must await a future study that incorporates all gempylids and trichiurids.

Character 27. In the outgroups, the posterior tip of the pterotic terminates in front of the posterior margin of the neurocranium. Trichiurids have a longer pterotic with the posterior tip terminating beyond the posterior margin of the neurocranium. In *Lepturacanthus* and *Trichiurus*, the pterotic extends as far as the first vertebra and, in some specimens, past the anterior margin of the second vertebra. All specimens of *Aphanopus*, *Benthodesmus*, *Eupleurogrammus*, *Evoxymetopon*, and *Lepidopus* analyzed have a pterotic extending as far as the second vertebra. Senta (1975) noted that in *Tentoriceps*, the pterotic processes are well developed and extend beyond the posterior end of the supraoccipital. In fact, the pterotic of *Assurger* and *Tentoriceps* extends as far as the third vertebral element. However, the length of the pterotic among the trichiurids is variable and dependent on the size of the specimens. In this study I use this character as a dichotomy in which the states are categorized ac-

cording to whether the pterotic extends past the posterior margin of the neurocranium or not.

INTERCALAR. The intercalar serves as the point of attachment for the ligament connecting the anteroventral articular process of the posttemporal to the neurocranium. Ventrally, it joins the exoccipital and is overlapped by the anterolateral corner of this bone. It is strongly fused to the pterotic dorsally, and it may articulate with the posterodorsal corner of the prootic anteriorly.

In the trichiurids and outgroups analyzed, the intercalar varied in shape from truncated to pointed. In *Assurger*, the exoccipital and the intercalar form a plate that appears pointed. *Tentoriceps* has an intercalar that is pointed but separate from a posteriorly directed projection on the exoccipital. Russo (1983: character 27) also noted that among the gempylids, *Diplospinus*, *Lepidocybium*, *Neoepinula*, *Paradiplospinus*, *Ruvettus*, *Thyrsoites*, *Thyrsoitops*, and *Tongaichthys* have an intercalar with a flat or slightly rounded posterior end. However, the shape of the posterior margin on the intercalar is highly variable and dependent on the size and degree of ossification of the specimens. In the trichiurids, except *Assurger*, and the outgroups, the intercalar is flat posteriorly and does not extend past the posterior margin of the neurocranium. *Assurger* is unique in that the intercalar is extremely long and extends posteriorly to reach a position above the second vertebra.

Character 28. Russo (1983: character 26) noted that the intercalar on *Diplospinus* and *Paradiplospinus* is confined to the ventral surface of the neurocranium and is not visible in dorsal view (a unique condition among gempylids). In *Gempylus*, *Nesiarchus*, and the trichiurids, the intercalar is reduced but visible dorsally. Although the condition at the outgroup node is equivocal, I follow the conclusion of Russo (1983) and consider the condition present in all gempylids, except *Diplospinus* and *Paradiplospinus*, to be plesiomorphic.

SPHENOTIC. The sphenotic joins the frontal anteriorly forming the frontosphenotic shelf. Posteriorly, the sphenotic joins the pterotic, whereas anteromedially it joins the pterosphenoid. Ventrally, the sphenotic articulates with the prootic. In dorsal view, the lateral margin of the sphenotic shelf bears a laterally directed process that accepts the anterior articular condyle of the hyomandibula. The morphology of this bone is similar among the taxa analyzed in this study.

PROOTIC. The prootic is a paired bone; each unit articulates anteriorly with the basisphenoid and with each other. The juncture of the two units of the prootic along their ventral margins forms the anterior portion of the posterior myodome (Collette and Chao, 1975). The prootic joins the basioccipital, exoccipital, and intercalar posteriorly. It articulates dorsally with the pterotic and sphenotic and ventrally with the parasphenoid. Allis (1903) described the trigeminofacial chamber as the area under the lateral arch of the prootic, which encases

the prootic foramen. All trichiurids and outgroups bear a prootic arch forming a foramen that connects the trigeminofacial chamber with the anterior half of the myodome. The morphology of this bone is similar among the taxa analyzed in this study.

Basicranial Region

EXOCCIPITAL. The exoccipital is a paired bone partially forming the foramen magnum. It bears an occipital condyle, which articulates with the atlas vertebra. This bone articulates with the basioccipital ventrally, the intercalar and supraoccipital dorsally, and the prootic anteriorly. Dorsally, it also joins the pterotic and the epiotic. In most trichiurids, the dorsomedial margins of the exoccipital do not meet each other, leaving an opening that runs from the posterior tip of the supraoccipital to the dorsal margin of the foramen magnum. In some specimens the dorsomedial margins bear cartilaginous edges that abut each other. An anterior glosso-pharyngeal foramen (Allis, 1903) is present close to the prootic, whereas posterior to this a second foramen is present for the vagus nerve (Russo, 1983).

The exoccipital ridge of the genus *Assurger* appears as an extremely elongate process. This elongate process is formed by the posterior extension of the intercalar and the exoccipital; its posterior tip reaches above the second vertebral element. Although it is possible that the extreme elongation of the exoccipital is not independent of the elongation of the intercalar, both conditions are treated separately and considered autapomorphies for the monotypic genus *Assurger*.

The exoccipital of *Eupleurogrammus* is unique in that it has two small, laterally directed processes on the dorsal face of the occipital condyle. The ventral process bears a small and poorly ossified intermuscular bone (the cephalic intermuscular bone of Collette and Chao, 1975). None of the outgroups, or the rest of the trichiurids, has such a modification on the exoccipital.

Character 29. Russo (1983: character 29) noted that *Diplospinus*, *Nealotus*, and *Paradiplospinus* are characterized by the presence of a ridge on the exoccipital, which is short and does not reach the vagus foramen. This ridge extends from the pterotic, crosses the intercalar, and reaches the exoccipital. In the rest of the gempylids and the trichiurids, the exoccipital ridge extends as a shelf-like structure over the intercalar, reaching the vagus foramen on the exoccipital. Although the condition at the outgroup node appears to be equivocal, I consider the presence of an exoccipital ridge that reaches the vagus foramen to be the plesiomorphic condition because it is present in all gempylids, except *Diplospinus*, *Nealotus*, and *Paradiplospinus*.

BASIOCCIPITAL. The basioccipital is a median bone forming the posteroventral corner of the neurocranium and the saccular bulla. Internally, it forms the lateral and ventral walls of the posterior

myodome (Collette and Russo, 1984). The basioccipital also forms the ventral edge of the foramen magnum and bears a concave facet for articulation with the atlas vertebra. It articulates anteriorly with the prootic and the parasphenoid. Dorsally, it joins the exoccipital. The morphology of this bone is similar among the taxa analyzed in this study.

PARASPHENOID. The parasphenoid joins the vomer anteriorly, and it articulates with the lateral ethmoid on the posterior wall of the ethmoidal region. Posteriorly, it articulates with the basisphenoid, the prootic, and the basioccipital, in that order. Its articulation with the prootic is by two dorsolateral extensions that form part of the anteroventral wall of the posterior myodome (Collette and Chao, 1975). The morphology of the parasphenoid is similar among the trichiurids and outgroups.

PECTORAL GIRDLE

The pectoral girdle is formed by those bones that support the pectoral fin rays and connect the pectoral fin to the neurocranium (Fig. 18).

Supratemporal

The supratemporal is positioned ventrolaterally to the dorsal articular process of the posttemporal (Fig. 19). The supratemporal of the trichiurids is characterized by three branches that bear laterosensory canals. The posterior branch forms the junction between the temporal canal in the posttemporal bone and the system of canals in the skull (Coombs et al., 1987). The anteroventral branch joins the temporal canal with the dorsal pore in the pterotic bone. The anterodorsal branch carries the supratemporal division of the temporal canal (Coombs et al., 1987) onto the parietal region. All the trichiurids and outgroups have a tripartite supratemporal bone with an elongate anterodorsal arm. However, the supratemporal of the specimens of *Tentoriceps* examined have a poorly developed partition between the two anterior canals. One specimen of *Tentoriceps* has a simple, longitudinal, tube-like supratemporal on the right side followed anteriorly by another unbranched, longitudinal, tube-like ossification. In contrast, the left side of the supratemporal shows a tube with three pores, but the anterodorsal branch is not extremely elongate. Russo (1983) indicated that in the gempylids, the elongate dorsal branch on the supratemporal represents the medial extrascapular, which has become fused to the dorsal branch of the supratemporal. The morphology of this bone is similar among the taxa analyzed in this study.

Posttemporal

The posttemporal has three arms or articular processes: the dorsal articular process attaches to the dorsal surface of the epiotic; the anteroventral articular process bears a ligamentous attachment to the intercalar; the posteroventral articular process

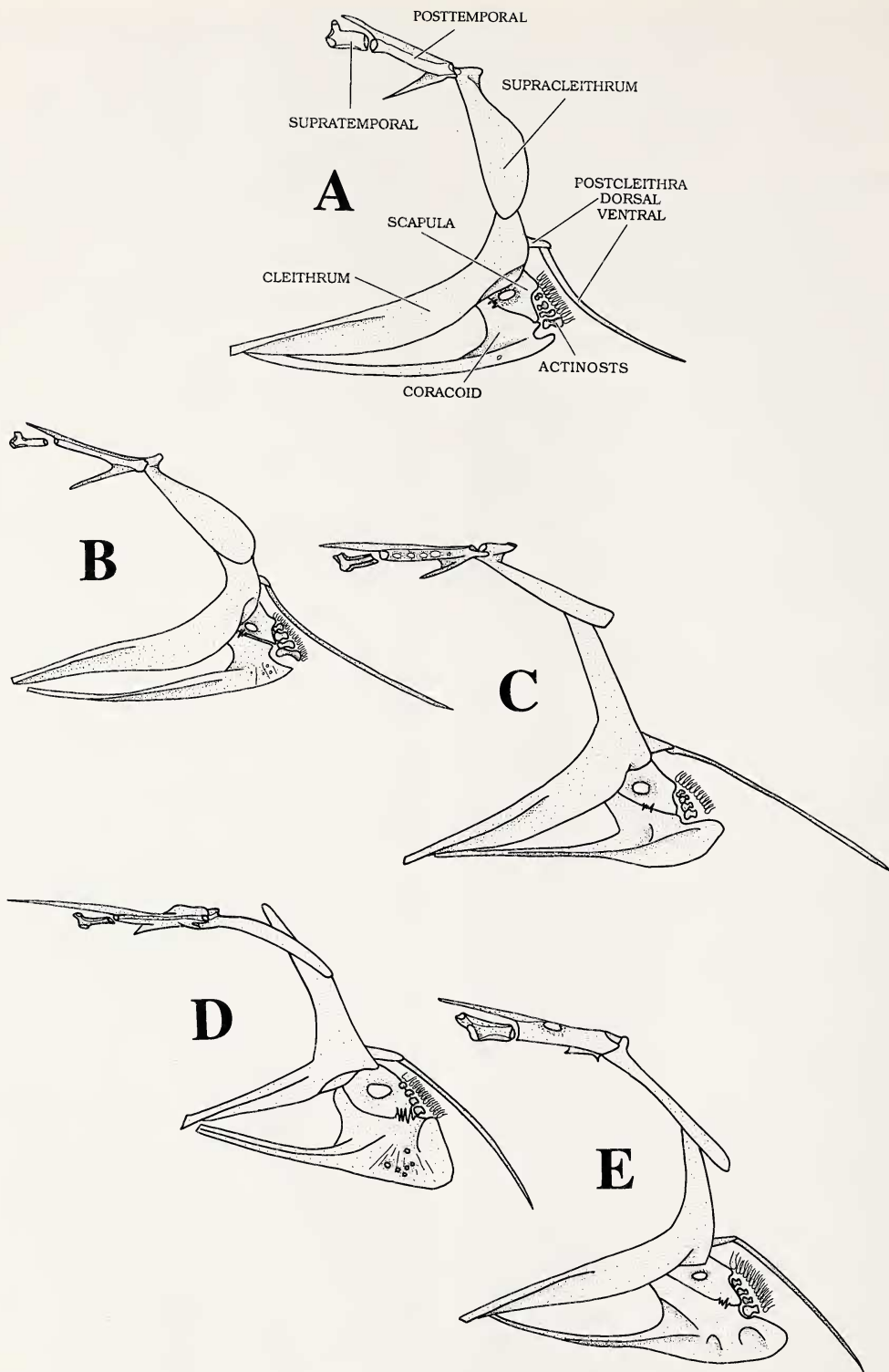


Figure 18. A-E. Lateral view of the left pectoral girdle: (A) *Diplospinus multistriatus*; (B) *Paradiplospinus antarcticus*; (C) *Aphanopus carbo*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*.

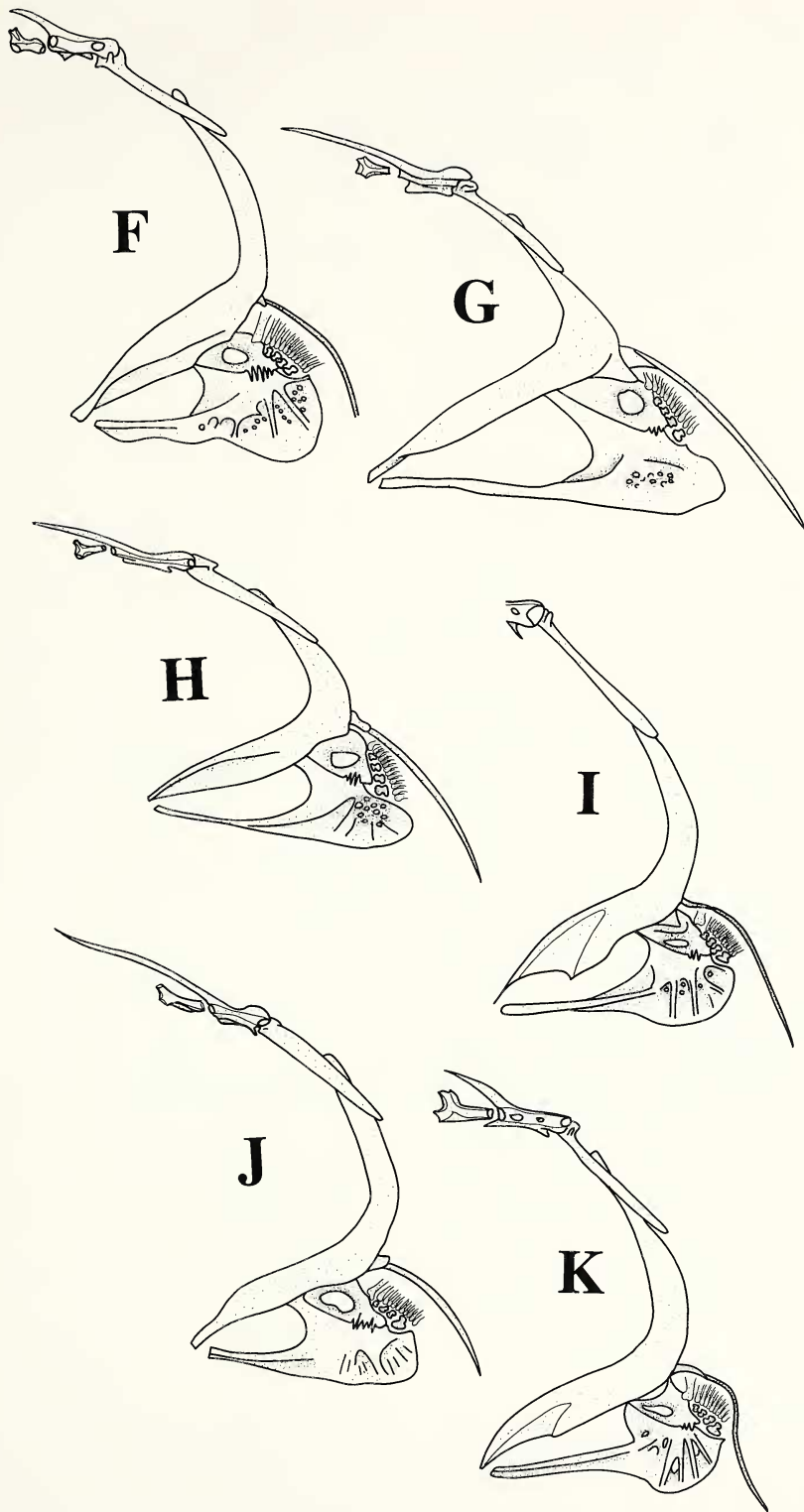


Figure 18. F-K. Lateral view of the left pectoral girdle: (F) *Eupleurogrammus glossodon*; (G) *Evoxymetopon taeniatus*; (H) *Lepidopus fitchi*; (I) *Lepturacanthus savala*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.

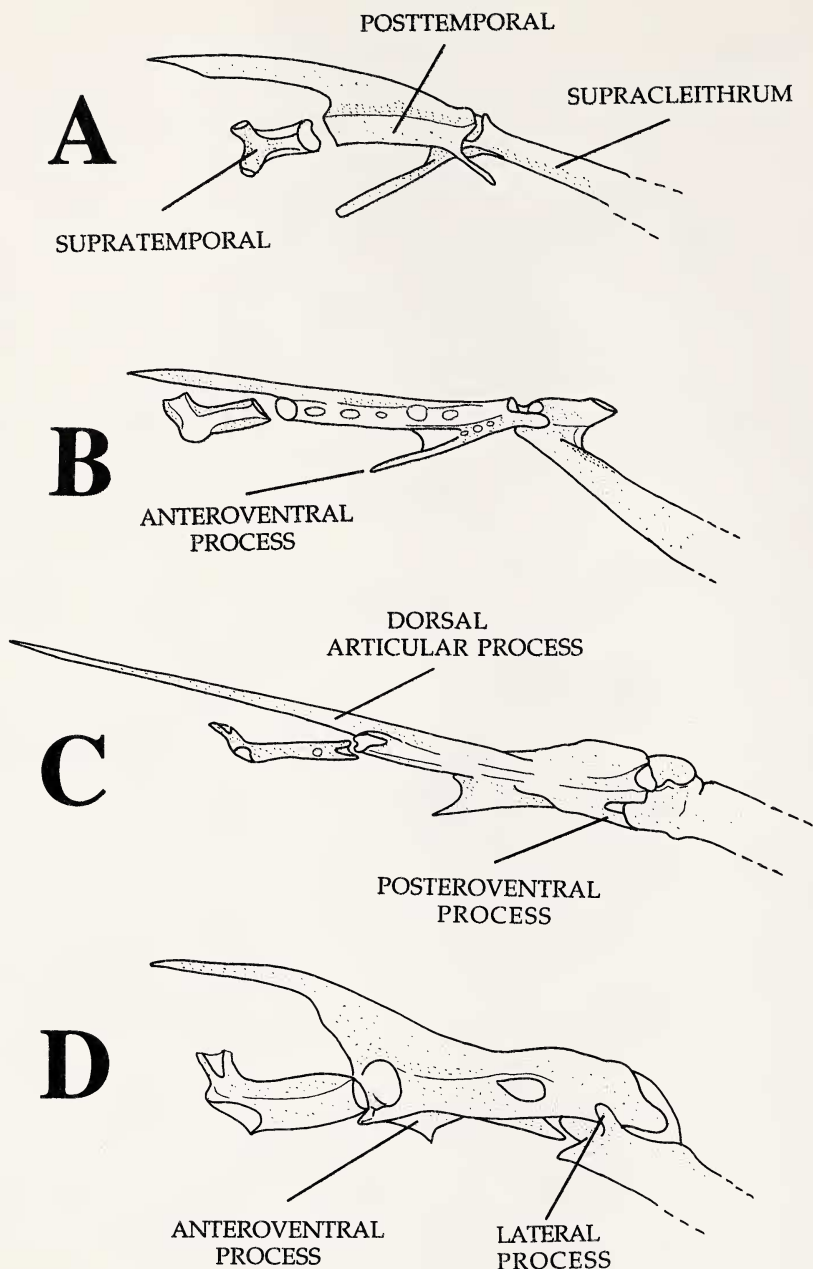


Figure 19. Lateral view of the left supratemporal, posttemporal, and the articular head of the supracleithrum: (A) *Gempylus serpens*; (B) *Aphanopus carbo*; (C) *Assurger anzac*; (D) *Eupleurogrammus glossodon*.

overlaps, or is attached by ligaments, to the dorsal articular head of the supracleithrum laterally. The posterior margin of the posttemporal overlaps the articular head of the supracleithrum laterally. This bone carries the temporal canal of the laterosensory canal system. It joins the canals in the supratemporal with the system of trunk canals in the body (Coombs et al., 1987).

Character 30. *Assurger*, *Evoxytmetopon*, *Lepi-*

dopus, and *Tentoriceps* are characterized by having an extremely elongate dorsal articular process, which extends past the anterior margin of the supratemporal and is at least twice the length of that bone (Fig. 19C). All the other trichiurids and the outgroups have a dorsal articular process that is short and terminates before or shortly after the anterior tip of the supratemporal (Fig. 19A, B, D).

Character 31. All the trichiurids, except *Aphan-*

opus, share the presence of a short posteroventral process on the posttemporal that is in direct contact, or in contact via ligamentous association, with the articular head of the supracleithrum (Fig. 19C, D). *Gempylus* bears a well-developed rod-like posteroventral process, but this condition is not comparable to that described for most trichiurids (Fig. 19A). In the trichiurids, the process is flat in cross section, further reduced in size, and more posteriorly directed and abuts the supracleithrum medially or bears a ligamentous connection with its articular head. In contrast, in *Gempylus* the posteroventral process is round in cross section and well developed and extends ventrally, and it is not in contact or close association with the articular head of the supracleithrum. *Aphanopus*, *Diplospinus*, *Nesiarchus*, and *Paradiplospinus* lack a posteroventral process (Fig. 19B).

Character 32. Russo (1983: character 69) identified the presence of a thin, rod-like anteroventral articular process as a synapomorphy of *Diplospinus*, *Gempylus*, and *Paradiplospinus*. He concluded that the presence of this process represents the plesiomorphic state characteristic of all the other gempylids, including *Nesiarchus*. The difference in the shape of the anteroventral articular process between *Nesiarchus* and the other outgroups (robust versus thin and rod-like) is difficult to evaluate. However, the anteroventral articular process of the trichiurids, except *Aphanopus*, is clearly different. It is elongate and well developed in the outgroups plus *Aphanopus*, and it is reduced in the rest of the trichiurids. In addition, the process originates at the posterior corner of the posttemporal of the outgroups plus *Aphanopus* (Fig. 19A, B), whereas in the trichiurids it originates close to or on the anterior half of the canal portion of the posttemporal, never at the posterior corner of the bone (Fig. 19C, D). Within the trichiurids, *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus* have an anteroventral process that originates separately from the origin of the posteroventral process. In contrast, *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* bear a reduced anteroventral process that originates from a common ventral ridge with the posteroventral process.

Character 33. The posterodorsal corner of the posttemporal in all the trichiurids, except *Aphanopus* and *Benthodesmus*, is expanded and plate-like (Fig. 19C, D). In *Aphanopus*, *Benthodesmus*, and the outgroups, the posterior end of the posttemporal is tube-like and does not have a plate-like expansion (Fig. 19A, B).

Supracleithrum

The posterior half of the supracleithrum in all the outgroups is expanded; the space between the margins of the supracleithrum is narrow anteriorly and wide posteriorly, giving the bone an ovoid appearance. All the trichiurids are characterized by having a supracleithrum with a posterior half that is not

expanded and in which the margins are nearly parallel throughout its length. Russo (1983: character 71) noted that *Gempylus* is characterized by having a supracleithrum with an elongate shape more similar to that described for the trichiurids in this study. He warned, however, that assignment of shapes to discrete categories and their subsequent polarization may be unwarranted. In addition, he suggested that ontogenetic changes in the shape of this bone weaken the argument for the categorization of this character. I agree with Russo (1983) that the categorization of this character is difficult, and I do not include it in the data matrix of this study.

Character 34. Russo (1983: character 72) noted that the gempylids *Diplospinus*, *Paradiplospinus*, *Promethichthys*, and *Thyrsites* have a posteriorly expanded process on the head of the supracleithrum, which bears a canal and transmits the lateral line to the posttemporal. The specimens of *Nesiarchus* examined in this study also have a canal bearing a posteriorly expanded process, whereas those of *Gempylus* and the trichiurids *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* lack a canal (Fig. 19A, D). The rest of the trichiurids, except *Aphanopus*, bear a posteriorly expanded head on the supracleithrum, with a semienclosed canal (Fig. 19C). *Aphanopus* shares a condition similar to that of the outgroups, except *Gempylus*, in which the articular head of the supracleithrum is posteriorly expanded and bears a completely enclosed canal (Fig. 19B).

Character 35. *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* bear a lateral process on the articular head of the supracleithrum that extends dorsally (Fig. 19D). This dorsally directed lateral process is well developed in *Lepturacanthus* and *Trichiurus*, but extremely reduced in *Eupleurogrammus*. The lateral process is absent in all the other trichiurids and the outgroups (Fig. 19A–C).

Character 36. The articular head of the supracleithrum in *Assurger*, *Eupleurogrammus*, *Lepidopus caudatus*, *L. fitchi*, and *Tentoriceps* bears a small anteroventral process (Fig. 19C, D). The rest of the trichiurids and the outgroups lack this process (Fig. 19A, B). However, although this condition is included as a character in the analysis, the validity of this character is questionable because the anteroventral process is quite variable in size within the five taxa above.

Cleithrum

The main body of the cleithrum is formed by two longitudinal shelves that meet along their anterior margins and run parallel to each other. The scapula, coracoid, and dorsal postcleithrum articulate on the medial longitudinal shelf of the cleithrum. The two units of the cleithrum meet at their anteroventral tips.

The medial shelf of the cleithrum extends posteriorly and overlaps the anterior margin of the scapula laterally. This extension varies in shape from

round to triangular. Starks (1911) described a thickening on the lower part of the cleithrum in an Atlantic specimen of *Trichiurus lepturus*. He concluded that the bone structure was not similar to that of the hyperostosis of the supraoccipital.

Scapula

The scapula supports three of the four actinosts on its posterior margin. A scapular foramen is present and variable in size and shape within species. An actinost process or posterodorsal facet accepts the first fin ray of the pectoral fin. The morphology of this bone is similar among the genera analyzed in this study.

Coracoid

The coracoid is a paired bone that articulates dorsally with the scapula and anteriorly with the cleithrum. It bears an elongate anteroventral process, which attaches to the anteroventral tips of the cleithrum. It supports the fourth actinost on its posterodorsal corner.

Character 37. Posteroventrally, all trichiurids have a coracoid with a well-developed plate bearing a convex ventral margin that extends beyond the posterior margin of the fourth actinost. The outgroups lack a posteroventral plate, and they have a flat ventral margin on the coracoid that ends before the fourth actinost.

Actinosts

The actinosts are four pairs of bones that support the bases of the pectoral fin rays. The dorsal-most actinost is numbered as the first and is the smallest of the series. The other three actinosts are each greater in size, with the fourth being the largest. The first three articulate with the posterior margin of the scapula, whereas the fourth articulates with the posterodorsal corner of the coracoid, or partially between the coracoid and the scapula. The morphology of these bones is similar among the genera analyzed in this study.

Postcleithrum

The postcleithrum includes two pairs of elongate bones. The first pair, or dorsal postcleithrum, attaches to the posteromedial surface of the cleithrum above the scapula. The second pair, or ventral postcleithrum, attaches to the posterior tip of the dorsal postcleithrum and extends posteroventrally into the hypaxial musculature.

The trichiurids and the outgroups have a dorsal postcleithrum that is short and crooked, or sigmoid-shaped, and a ventral postcleithrum with a broad lamellar articular head and a long, styliform descending process. *Gempylus* is characterized by a ventral postcleithrum that is longer than the height of the pectoral girdle (i.e., from the dorsal margin of the posttemporal to the ventral margin of the cleithrum), whereas all the trichiurids and the rest

of the outgroups bear a shorter ventral postcleithrum.

Pectoral Fin Rays

Nakamura and Parin (1993) noted that *Trichiurus gangeticus* Gupta 1966 bears serrations on the first pectoral ray. They considered the first pectoral ray in *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* to be a spine. However, cleared and stained specimens show that the first ray of all the trichiurids and the outgroups is bilaterally divided and that it has an open base that embraces a cartilaginous knob above the first actinost. These characteristics identify this first pectoral element as a soft ray.

Character 38. The relative lengths of the pectoral fin rays vary among genera and account for the differences in shapes of the pectoral fin. In the outgroup genera *Diplospinus* and *Paradiplospinus* and in the trichiurids *Aphanopus*, *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus*, the posterior rays are longer. In contrast, in the outgroup *Gempylus* and in the trichiurids *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*, the anterior rays are the longest. The specimens of *Nesiarchus* analyzed in this study have pectoral fins with longer posterior rays. However, in the drawing of an adult *Nesiarchus* presented by Nakamura and Parin (1993: 35), the condition appears to be reversed. I have not been able to confirm the variation in this condition, and so I consider the state present in the specimens used in my study as characteristic of this genus.

PELVIC GIRDLE

The pelvic girdle is composed of the basipterygium, which supports the fin rays (Fig. 20). Stiassny and Moore (1992) divided the basipterygium into a central part, anterior and posterior processes, and ossified wings. The central part bears cartilaginous tips anteriorly and an articular surface for the fin rays posteriorly. The posterior and anterior processes extend posteriorly and anteroventrally from the articular surface, respectively. The central part might bear four wings of membranous origin: external dorsal, external ventral, internal, ventral.

All the taxa analyzed in this study, except *Benthodesmus*, *Evoxymetopon*, *Lepidopus*, and *Nesiarchus*, have a posterior process that is extremely elongate and extends well past the distal tip of the pelvic scale or spine. In all of these taxa, the posterior process is about the same length as the central part. This process is greatly reduced in size in *Benthodesmus* and *Nesiarchus*, and it does not extend past the tip of the external fin rays. The posterior process is of about the same length as the central part in *Benthodesmus*, whereas it is about one-third the length of the central part in *Nesiarchus*. The posterior process of *Evoxymetopon* and *Lepidopus* is elongate and about the same length as the central part. In *Evoxymetopon*, *L. caudatus*, and *L. fitchi*, it is about the same length as the

scale-like spine. In *L. altifrons*, the posterior process is slightly larger than the scale-like spine. The length of the posterior process relative to the central part is quite variable and difficult to categorize objectively.

In all the taxa analyzed, except *Aphanopus*, the anterior process appears to be absent or extremely reduced. The length of the external ventral wing and the degree of thickness of its ventral margin are variable. It is well ossified and thick in the outgroups *Diplospinus*, *Gempylus*, and *Paradiplospinus* and the trichiurids *Benthodesmus tenuis*, *Eupleurogrammus*, and *Tentoriceps*. In contrast, it is not well ossified in *Assurger*, *Evoxymetopon*, *Lepidopus*, and the outgroup *Nesiarchus*. The length of the external ventral wing is quite variable and varies from less than half of the length (*Diplospinus* and *Paradiplospinus*) to more than half and up to about equal the length of the central part (all other taxa analyzed). Some specimens of *Tentoriceps* have an external ventral wing that extends only half the length of the central part, whereas in others it extends throughout the whole central part. The length of the external ventral wing is also variable among the species of *Benthodesmus*.

The degree of extension of the ventral margin of the external ventral wing is extremely variable and dependent on the degree of ossification and size of the specimens. Potthoff (1980) reported that in *Coryphaena* Linnaeus 1758, the structures of membranous origin in the pelvic girdle (anterior process and wings) develop last, after the ossification of the central part. Thus, categorization of the extent and degree of ossification of the external ventral wing is difficult, and the character is not included in this analysis.

Character 39. The outgroups are characterized by the presence of a well-developed basipterygium. In the trichiurids, the basipterygium has become extremely reduced or completely lost as it occurs in *Lepturacanthus* and *Trichiurus*.

Although the basipterygium of *Aphanopus* is reduced to a small internal plate, some parts are discernible under the microscope. Anteriorly the basipterygium bears what appears to be an extremely reduced central part. The central part appears as two unfused, short processes that are slightly inclined dorsally. In *Aphanopus* and the outgroup *Paradiplospinus*, the pelvic girdle bears a single spine in the juveniles, but the spine becomes extremely reduced in the adult where only the internal basipterygium remains.

Character 40. *Diplospinus* bears a pelvic fin with an ornamented scale-like element and no soft rays. The lateral margins of the scale-like element in *Diplospinus* are serrate. However, although this condition is described as different from that present in the trichiurids with a pelvic fin (i.e., presence of an unornamented scale-like element), one must be careful because the largest specimen of *Diplospinus* available in this study was only 193 mm SL. Nakamura and Parin (1993) reported that this species

is common up to 200 mm and that it reaches a maximum of 330 mm SL. It is possible that larger specimens of *Diplospinus* have lost the ornamentation of the lateral margins of this scale-like element. In contrast, *Gempylus* and *Nesiarchus* have stronger, better developed pelvic girdles with one spine and from three to four and one to five soft rays, respectively. *Eupleurogrammus* and *Tentoriceps* have a reduced scale-like element and no soft rays. *Benthodesmus* bears a scale-like element and a single soft ray. *Assurger*, *Evoxymetopon*, and the species of *Lepidopus* analyzed in this study have a scale-like element and two soft rays. *Lepturacanthus* and *Trichiurus* lack the pelvic girdle and fin elements.

Character 41. The position of the basipterygium relative to the pectoral girdle has been used as a taxonomic character for the identification of some trichiurid taxa (Nakamura and Parin, 1993). *Eupleurogrammus* and *Tentoriceps* are characterized by an abdominal basipterygium that is located posteriorly, well past the pectoral girdle, including the tip of the ventral postcleithrum. The outgroup taxa analyzed in this study are characterized by having a basipterygium that is located under the pectoral girdle. *Aphanopus*, *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* have a basipterygium that is located completely or partly under the pectoral girdle (including the ventral postcleithrum). The basipterygium of adult *Aphanopus* is extremely reduced and located under the coracoid, anterior to the actinosts. The pelvic girdle of *Benthodesmus* is also reduced in size, and its position is variable among species. Nakamura and Parin (1993) used the position of the base of the pelvic-fin rays with respect to the pectoral-fin rays as a character for the identification of the different species of *Benthodesmus*. In the cleared and stained specimens of the species of *Benthodesmus* analyzed in this study, the basipterygium is always located under the pectoral girdle anterior to the ventral postcleithrum. *Assurger*, *Evoxymetopon*, and *Lepidopus* have a basipterygium in which the posterior process is partially or completely located posterior to a vertical | from the ventral tip of the ventral postcleithrum. However, in *Assurger*, *Evoxymetopon*, *Lepidopus*, and those species of *Benthodesmus* not available for this study, in which the base of the pelvic-fin rays is posterior to the pectoral-fin base, the articular facet of the basipterygium is always anterior to the tip of the ventral postcleithrum.

Character 42. In all the outgroups the central part of the basipterygium is dorsally inclined and extends anteriorly between the cleithrum and coracoid bones. Stiassny and Moore (1992) described this condition among percomorphs and noted that the central part of the pelvic girdle attaches to the cleithrum or coracoid by ligaments. They also concluded that among the acanthomorphs, this condition can be considered as apomorphic, with the pleiomorphic condition represented by a pelvic girdle that is parallel to the ventral body wall. All the

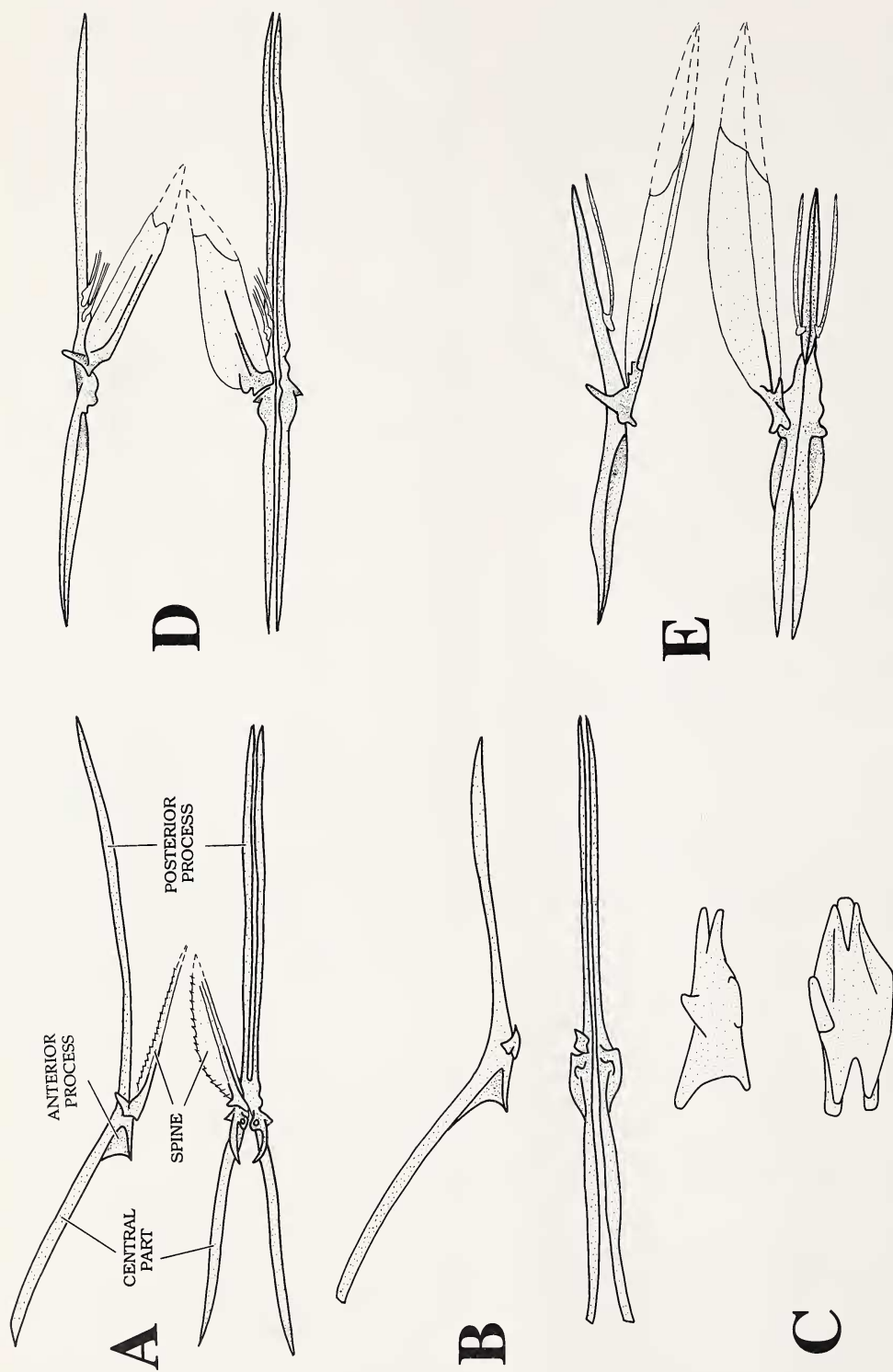


Figure 20. A–E. Lateral and ventral views (top and bottom, respectively) of the pelvic girdle: (A) *Diplospinus multistriatus*; (B) *Paradipllospinus antarcticus*; (C) *Aphanopus carbo*; (D) *Assurger anzac*; (E) *Benthodesmus tenuis*.

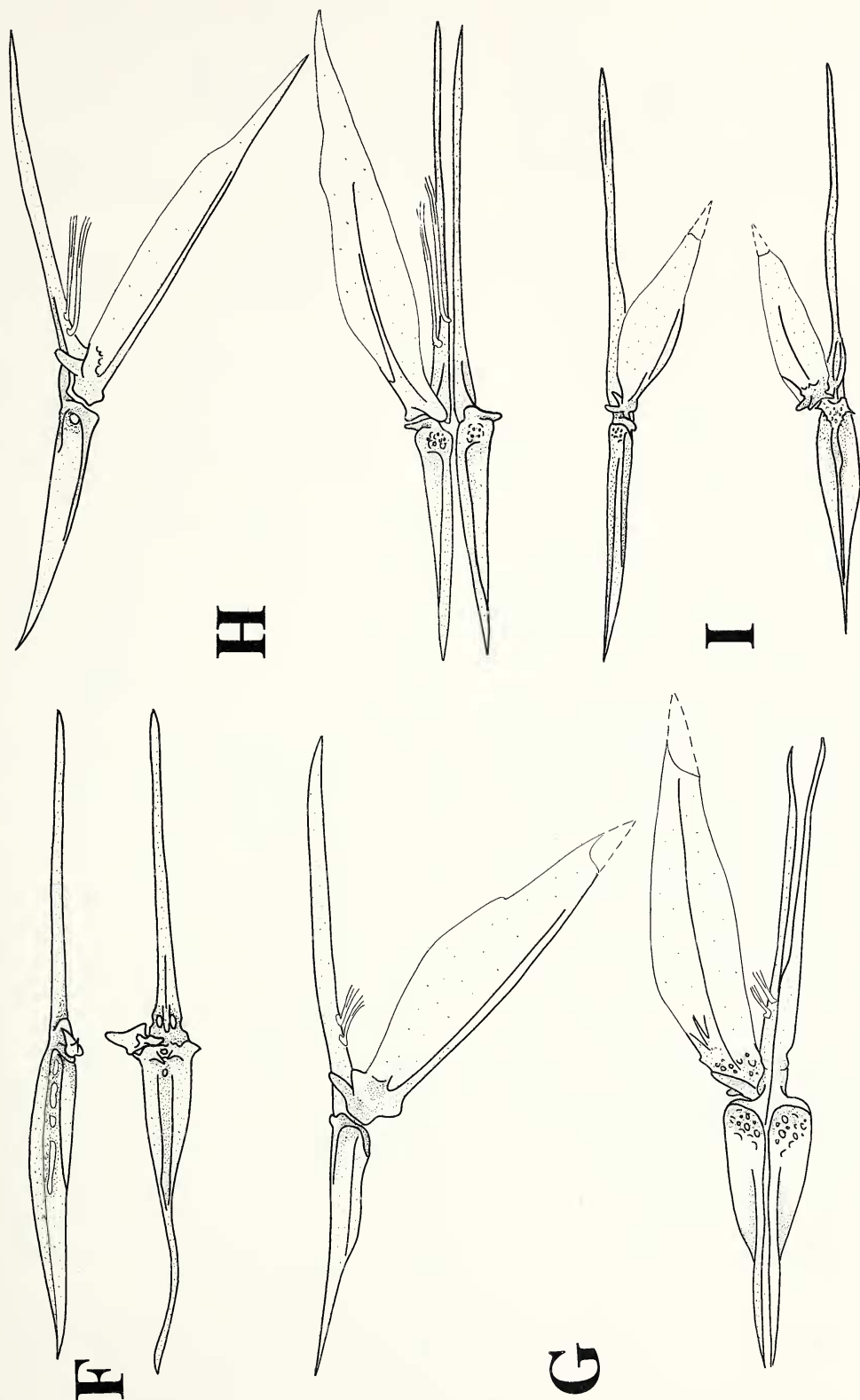


Figure 20. F-I. Lateral and ventral views (top and bottom, respectively) of the pelvic girdle: (F) *Eupleurogrammus glossodon*; (G) *Evoxynotopon taeniatus*; (H) *Lepidopus fitchi*; (I) *Tentoriceps cristatus*.

trichiurids, except *Lepturacanthus* and *Trichiurus*, are characterized by having a basipterygium that is parallel or nearly parallel to the central body wall. The central part of the basipterygium in *Aphanopus*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* may be slightly inclined dorsally. However, the condition in these genera is not comparable to that present in the outgroups, in which the central part is extremely inclined and extends between the cleithrum and coracoid.

Character 43. *Eupleurogrammus* and *Tentoriceps* are characterized by having a basipterygium that is completely fused along its longitudinal axis. In *Benthodesmus*, the posterior process appears to be fused, whereas the central part is not. The reduced basipterygium of *Aphanopus* bears a central part that appears as two unfused processes. In contrast, *Assurger*, *Evoxymetopon*, *Lepidopus*, and the outgroups have a basipterygium that is not fused along its entire longitudinal axis.

AXIAL SKELETON

Vertebral Column

In the outgroups and the trichiurids, except *Tentoriceps*, the first rib is present on the third precaudal centrum (Fig. 21). *Tentoriceps* is the only taxon analyzed in which the first rib is on the second precaudal centrum. The trichiurids, except some of the specimens of *Lepidopus fitchi*, are characterized by the presence of ribs in all the rest of the precaudal centra. In the outgroups, some posterior precaudal centra bear haemal ribs that articulate laterally with a fully formed haemal arch. I found no evidence of haemal ribs in the posterior precaudal centra of the trichiurids, except in *Lepidopus fitchi*, in which the last two to four precaudal centra bear haemal ribs. However, in some specimens of *Lepidopus fitchi*, the last haemal ribs may be fused at their tips.

The neural prezygapophyses are well developed in the outgroups and the trichiurids. Those in *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* are larger in size. In contrast, the neural postzygapophyses are smaller than the prezygapophyses. The haemal pre- and postzygapophyses are well developed in the caudal centra of all the outgroups and trichiurids. In *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*, the haemal pre- and postzygapophyses are more vertically directed when compared with the rest of the taxa analyzed.

Lateral apophyses (extending on the frontal plane of the vertebral column) are present in the posterior-most precaudal centra and most of the caudal centra of the trichiurids. In the trichiurids with a caudal fin, the last caudal centrum bearing a lateral apophysis is that which still maintains an articulation with a dorsal or anal pterygiophore, or both. The proximal shafts of a few of the last anal and dorsal pterygiophores have lost their direct articulation with the corresponding neural and haemal spines.

The specimens of *Benthodesmus tenuis* analyzed in this study have a few posterior caudal vertebrae that lack lateral apophyses, although they still maintain an articulation with the corresponding dorsal and anal pterygiophores. The last centrum bearing an articulation with the corresponding pterygiophores has lateral apophyses.

Those trichiurids lacking a caudal fin (i.e., *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*) also have lateral apophyses. The lateral apophyses are better developed along the anterior half of their respective centra. As one proceeds posteriorly, the length of the lateral apophyses increases, and the length is gradually reduced again in the posterior caudal vertebrae. The last lateral apophysis is on the last centrum maintaining an articulation with the dorsal and anal pterygiophores. In the posterior caudal centra, the lateral apophyses extend anteriorly onto the preceding vertebral element. These lateral apophyses are more elongate in *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* than in any of the other taxa analyzed. In *Eupleurogrammus*, the lateral apophyses become more vertically oriented as one proceeds posteriorly. As the lateral apophyses change orientation, the haemal prezygapophyses become reduced in size and appear to be replaced in position by the vertically oriented lateral apophyses. The outgroups, except *Gempylus*, lack or have extremely reduced lateral apophyses. *Gempylus* bears reduced lateral apophyses that do not extend past the anterior margin of their corresponding centra, as in the trichiurids.

Character 44. A characteristic of the trichiurids is the extreme elongation of their bodies. According to Nakamura and Parin (1993), the total number of vertebrae range from 57 to 64 in *Diplospinus*, 48 to 55 in *Gempylus*, 34 to 36 in *Nesiarchus*, 60 to 67 in *Paradiplospinus*, and 84 to 198 in the trichiurids. Collette et al. (1984: character 29) and Johnson (1986: character 16) utilized vertebral counts as a multistate character series. Johnson (1986) warned of the arbitrariness involved in categorizing the states of a meristic character. I agree with the conclusions of Carpenter et al. (1995) and consider their groupings among all the scombroids as a better representation of the distribution of vertebral numbers. Following the categorization of Carpenter et al. (1995) for all scombroids (with a slight modification to account for meristic data from this study and the literature), I consider the following character states with respect to the total number of vertebrae: 30 to 55 as state 0 among the gempylids (including *Gempylus* and *Nesiarchus*); 57 to 67 as state 1 among the gempylids (including *Diplospinus* and *Paradiplospinus*); 84 to 198 as state 2 for the trichiurids. Although this multistate character results in the assignment of an equivocal state at the outgroup node, I consider the condition present in the basal gempylids (i.e., gempylids minus *Diplospinus* and *Paradiplospinus*) as plesiomorphic.

Character 45. The first neural spine of all the

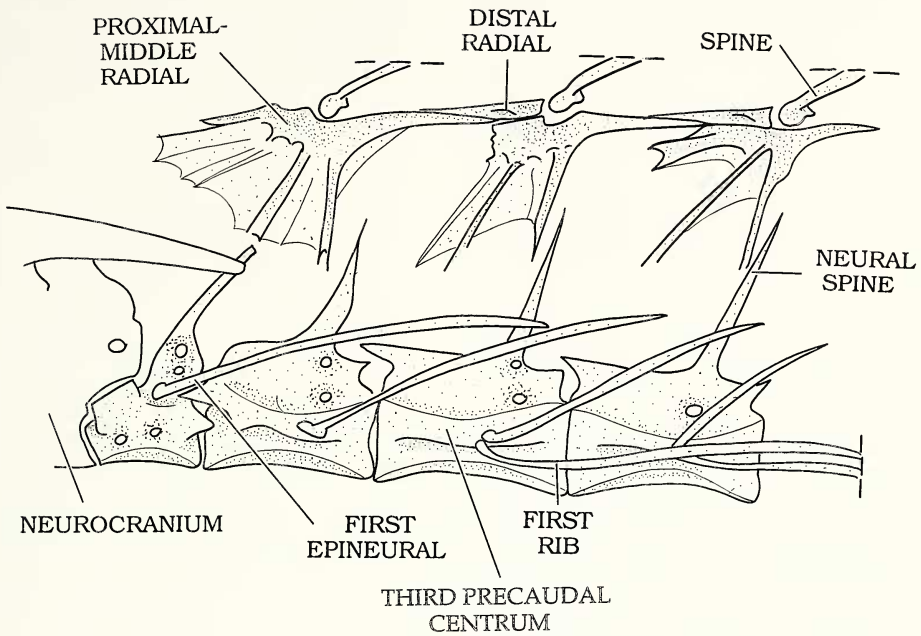
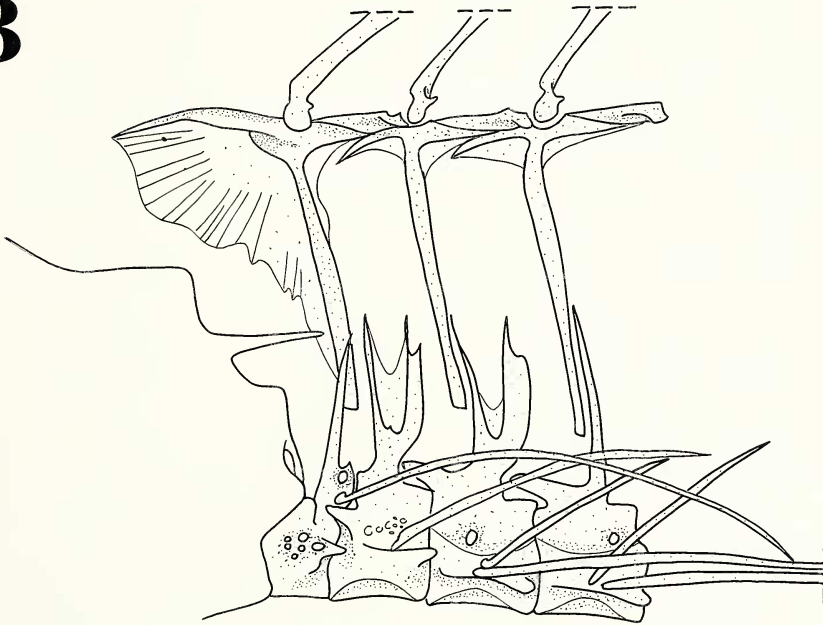
A**B**

Figure 21. Left view of the anterior elements of the axial skeleton: (A) *Benthodesmus tenuis*; (B) *Trichiurus lepturus*.

trichiurids analyzed is distally bifurcate, and the proximal-middle radial of the first dorsal pterygiophore partially fits between its tips. The condition has been described in *Trichiurus* (Fig. 21B) by Potthoff et al. (1986). The outgroups, except *Gem-*

pylus, have a first neural spine that is not bifurcate at its tip. In the specimen of *Gempylus* analyzed in this study, the first vertebral element bears an extremely reduced, distally bifurcate neural spine. However, the condition in *Gempylus* is not com-

parable to that of the trichiurids. The unfused tips might be part of the neural arch, which is never completely closed during their ontogeny. The proximal-middle radial of the first dorsal pterygiophore does not fit between the unfused tips of the first neural spine.

Character 46. In *Lepturacanthus* and *Trichiurus*, the neural spines of centra two and three are expanded and plate-like with their anterior and posterior margins well ossified and bearing pointed tips that give the neural spines a forked shape (Fig. 21B). *Assurger*, *Eupleurogrammus*, and *Tentoriceps* share the same condition, but the expanded neural spines are on centra two to four, two to five, and two to six, respectively. All of the neural spines in the outgroups and in the trichiurids *Aphanopus* and *Benthodesmus* are simple and not expanded (Fig. 21A). Most of the specimens of *Evoxymetopon*, *Lepidopus altifrons*, *L. caudatus*, and *L. fitchi* analyzed bear slightly expanded anterior neural spines (not including the first centrum), but they are not distally forked as in *Assurger*, *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*.

Intermuscular Bones

The intermusculars are segmental, serially homologous ossifications or ligaments in the myosepta of teleosts (Patterson and Johnson, 1995) that can be divided into myorhabdoi, epipleurals, epineurals, and epicentrals. Myorhabdoi, which occur only in a few teleosts, are not present in the trichiurids. Patterson and Johnson (1995) noted that epipleurals are absent in all acanthomorphs, except *Polymixia* Lowe 1838, *Velifer* Temminck and Schlegel 1850, and holocentrids. Epineurals appear as a series of bones or ligaments that develops in a rostrocaudal direction from the occipital region back. In the plesiomorphic condition, epineurals develop as outgrowths of the neural arches. In derived teleosts, epineurals have lost the ossified continuity with their respective neural arch and retain only a ligamentous attachment (Patterson and Johnson, 1995).

Epineurals are present in all the outgroups and the trichiurids, ranging from three to seven and articulating directly with the first three to seven vertebrae (Fig. 21). The first epineural originates on the neural arch of the first vertebral element, whereas the others originate farther ventrally on the head of the rib or the parapophyses. The distal margin of the anterior epineurals is forked in *Tentoriceps* and simple and pointed in other trichiurids and outgroups. However, *Evoxymetopon* and *Lepidopus* bear slightly expanded epineurals with a well-ossified central axis that supports two lateral thin plates.

In addition to the series of three to seven epineurals that articulate directly with the vertebrae, the outgroups are characterized by the continuation of the ossified epineural series farther back into the caudal region. *Nesiarchus* bears what appear to be

unattached epineurals from vertebrae 6 to 17 (the vertebral numbers are in reference to the position of the proximal tip of the epineural with respect to the vertebrae). These epineurals are simple, rod-like ossifications, with the exception of the epineurals on vertebrae 9 and 10, which are slightly forked proximally. In *Paradiplospinus*, the attached epineurals on vertebrae 4 to 6 are forked proximally. The anteromedial branch attaches to the corresponding centrum, whereas the anteroventral branch extends next to the preceding centrum. Dorsal to the seventh attached epineural there is a free, rod-like epineural similar in orientation and shape to the anteroventral branch and distal portion of the preceding epineurals. Farther posteriorly, *Paradiplospinus* bears simple, unattached, rod-like epineurals from vertebrae 8 to 59. I consider these apparently unattached epineurals as homologous with the anteroventral branches and distal portions of those anterior epineurals that are proximally forked. In *Diplospinus*, the unattached epineurals extend between vertebrae 6 and 54, and the attached epineurals of vertebrae 3 to 6 are forked. *Gempylus* bears three attached epineurals that articulate directly with the first three vertebrae (the first articulates at the base of the neural arch). The first two are simple and rod-like, but the third is forked proximally (i.e., the anteromedial branch attaches to the corresponding centrum and the anteroventral branch extends next to centrum 2). *Gempylus* is characterized by having the first unattached epineural originating anterior to the attached epineural of the first vertebra and medial to the supratemporal. The second epineural of *Gempylus* is also unattached; it is parallel to the distal portion of the first attached epineural, with its proximal tip lying above centrum 2. The next element of the series is represented by the anteroventral branch and distal portion of the forked epineural attached to centrum 3. Posterior to these few elements the rest of the epineurals are unattached, simple, and rod-like, with the series extending caudally to centrum 45. Although *Diplospinus*, *Nesiarchus*, and *Paradiplospinus* have no unattached epineurals originating anterior to centra 3 to 7, a series of ligaments parallel to the ossified, unattached epineurals extends anteriorly to these centra.

The epicentrals of teleosts develop in a rostrocaudal direction, lie in the horizontal septum, and are almost always simple rods (Patterson and Johnson, 1995). *Diplospinus*, *Gempylus*, and *Paradiplospinus* have a series of intermuscular bones that extend into the hypaxial musculature. These bones are simple, rod-like ossifications, and they are in reverse orientation to their unattached epineural counterparts. Their proximal tips appear to be unattached and lie laterally to their corresponding centrum. I consider this series of intermusculars as epicentrals. The proximal tips of the epicentrals originate next to centra 4 to 54 in *Diplospinus*, 3 to 45 in *Gempylus*, and 6 to 59 in *Paradiplospinus*. Although both of the epicentral series and most of

the epineurals appear to be unattached, it is possible that they have a ligamentous connection with their corresponding centra. The proximal tips of the unattached intermuscular bones in the outgroups are extremely thin, and I could not determine the presence of a ligamentous attachment at their proximal tips. Furthermore, the vertebral ranges described above are based on a single or a few representative specimens of each genus. Variation in these ranges was observed in those taxa for which more than one specimen was available. In this section, only the upper and lower limits of these ranges are presented. Thus, these meristics should not be taken as an absolute description of the distribution of intermusculars in these fishes.

Character 47. Presence or absence of unattached, ossified epineurals and epicentrals is considered as a multistate character. *Diplospinus*, *Gempylus*, and *Paradiplospinus* are characterized by the presence of unattached epineural and epicentral series that extend into the caudal region. *Nesiarchus* has a series of unattached epineurals that extends into the caudal region but lacks an epicentral series. Trichiurids bear a few attached epineurals, but they lack the series of unattached epineurals and epicentrals.

Dorsal Fins

Tucker (1953) indicated that the presence of a continuous dorsal fin in most trichiurids clearly sets them apart from *Aphanopus*, *Benthodesmus*, the gempylids, and other scombroids.

Character 48. *Aphanopus* and *Benthodesmus* have a notch on the dorsal-fin membrane that separates the two dorsal fins, whereas the rest of the trichiurids have a continuous dorsal-fin membrane. All gempylids have a well-developed notch that separates the soft and spinous portions of the dorsal fin.

Character 49. In the gempylids the spinous dorsal fin bears from 19 to 39 spines and its base is longer than that of the soft dorsal. Most trichiurids have a spinous dorsal fin with a base that is shorter than the soft dorsal. Within the trichiurids, *Aphanopus* has a spinous dorsal fin that bears from 38 to 45 spines and is only slightly shorter than the soft-dorsal portion. *Assurger* and *Benthodesmus* are both characterized by a spinous dorsal fin that bears 31 to 46 spines and is less than half of the length of the soft-dorsal portion. A further derived condition, where the spinous dorsal fin is extremely short with only three to 10 spines, could be hypothesized for all trichiurids, except *Aphanopus*, *Assurger*, and *Benthodesmus*. Nakamura and Parin (1993: 70) indicated that *Aphanopus* and *Benthodesmus* have from 38 to 45 and 31 to 46 dorsal-fin spines, respectively. They also reported that *Assurger* only has "a few weak anterior spines hardly differing from the soft rays." However, upon close examination of radiographs and cleared and stained specimens of *Assurger* I found that its dor-

sal fin is composed of 34 to 35 spinous rays. These rays are true spines in that they are unsegmented, median elements with a closed base bearing a central foramen. In contrast, the soft rays are usually segmented, bilaterally divided, and branched at their tips. The spinous rays can also be identified in the trichiurids and outgroups by the type of articulation with their respective pterygiophores. The bases of the spinous rays do not embrace the distal radial (extra distal "x" radial of Johnson, 1986: character 30).

Character 50. Johnson (1986) noted that the morphology and development of pterygiophores of the soft-dorsal and anal fins in the trichiurids is similar to that of spinous pterygiophores. The pterygiophores supporting spinous-dorsal rays in the gempylids and the trichiurids are composed of proximal-middle and distal radials, which articulate by extensive overlapping (Johnson, 1986: character 21). These proximal-middle and distal radials have a concave dorsal face. In *Gempylus* the proximal-middle radials are extremely concave dorsally and bear well-developed pointed corners in their middle portions. Furthermore, Johnson (1986: character 22) indicated that in the gempylids, the posterior facet of the spinous distal radials is convex and acts as an articular condyle for the concave ventral margin of the closed bases of the dorsal spines. This condition is also shared by the spinous-dorsal elements of the trichiurids.

Johnson (1986: character 30) noted that the bases of the soft rays in the dorsal and anal fins of trichiurids embrace an extra distal "x" element that develops, as a separate ossification, posterior to its corresponding distal radial. The pterygiophores of the soft-dorsal and anal fins in the outgroups utilized in this study also have a separate radial that is embraced by the bases of the soft rays. This element is similar in shape to the "x" radial described by Johnson (1986), which is embraced by the open bases of the soft rays of the trichiurids (Fig. 22). The "x" element in the trichiurid soft rays bears an anteroventrally projecting pedestal (anterodorsally in the anal-fin pterygiophores) that ends in a cartilaginous knob that articulates with the concave articular facet of the preceding distal radial. The "x" radial also bears two laterally directed wings posteriorly. In trichiurids, the "x" element is a single ossification. In the outgroups, the distal radial, which is embraced by the open base of the corresponding soft ray, is not ossified along its medial axis, but the posterolateral wings and the lateral faces of the anterior pedestal are ossified. Johnson (1986) considered the possibility that the "x" element, embraced by the bases of the soft rays in the trichiurids, is a neomorph. The ontogenetic data of Gago (1997) indicate that the extra distal radial of Johnson (1986) is not a neomorph. Ontogenetic series of the outgroup genera show that the trichiurids and gempylids share a similar pattern of development of their dorsal fin pterygiophores. The presence of only two radials (proximal-middle and dis-

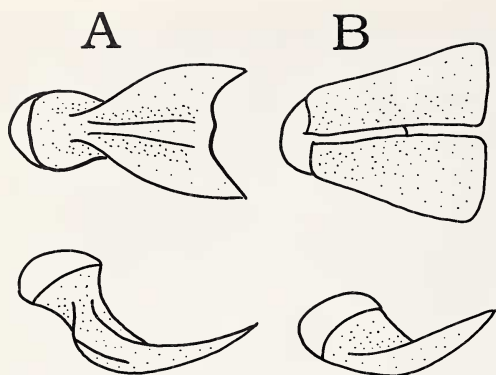


Figure 22. Ventral and lateral views (top and bottom, respectively; cartilage is not stippled) of the anal-fin 'x' radial of Johnson (1986) in adult: (A) *Trichiurus lepturus*, 288 mm TL; (B) *Paradiplospinus antarcticus*, 278 mm SL.

tal) supporting the soft rays of the dorsal fin in gempylids is the result of the fusion of the proximal and middle radials during development. In the trichiurids, the proximal and middle radials do not fuse during development and the adult retains three separate radials. Thus, the extra distal radial of Johnson (1986) appears to be homologous to the distal radial of other scombroids.

Günther (1860) and James (1960) reported hyperostosis of some of the dorsal proximal-middle radials in some specimens of *Lepidopus caudatus* and *Trichiurus lepturus*. James (1960) indicated that of the four species of trichiurids occurring in Indian waters (i.e., *Eupleurogrammus glossodon*, *E. muticus* (Gray 1831), *Lepturacanthus savala*, and *T. lepturus*) this condition was only present in *T. lepturus*. Radiographs of the holotype of *Evoxymetopon taeniatus* also show hyperostosis of some of the dorsal-fin proximal-middle radials. Smith-Vaniz et al. (1995) only listed the presence of hyperostosis in one species of trichiurid. To this list I add the report of hyperostosis on the dorsal-fin pterygiophores of *L. caudatus* and the new record of this condition in the holotype of *E. taeniatus*. The first dorsal pterygiophore of all the outgroups and the trichiurids bears a supernumerary spine and a second spine that articulates with the posterior facet of the distal radial.

Character 51. Johnson (1986: character 20) reported an extreme plate-like expansion of the proximal shaft of the first proximal-middle radial in the trichiurids (Fig. 21) and gempylids, except *Lepidocybium* and *Ruvettus*, which bear only a moderate expansion. In all trichiurids, except *Aphanopus* and *Benthodesmus*, this plate-like expansion of the first dorsal pterygiophore extends anteriorly above the occipital region of the neurocranium. The outgroups plus *Aphanopus* and *Benthodesmus* are characterized by a first proximal-middle radial

that does not extend onto the occipital region of the neurocranium.

In *Benthodesmus*, several of the anterior proximal-middle radials following the first pterygiophore also bear a plate-like extension on the anterior and posterior margins of the proximal shaft. The posterior margin of the plate-like extension is well ossified and, in conjunction with the obliquely oriented proximal shaft, gives the bone the appearance of an inverted "V." The tubular shaft bears a cartilaginous tip and lies free in the corresponding interneural space, whereas the posterior margin of the plate-like extension articulates with the neural spine of the subsequent vertebral element. As one proceeds posteriorly, the plate-like ossifications become smaller and the tubular margin shifts gradually and posteriorly until it comes in contact with the neural spine of the subsequent vertebral element.

All trichiurids, except *Aphanopus* and *Benthodesmus*, have a first dorsal proximal-middle radial with an elongate proximal shaft that fits primarily in the second interneural space. However, the anterior plate-like extension of the proximal shaft extends onto the occipital region and passes between the bifurcate tip of the first neural spine. *Aphanopus* and *Benthodesmus* have a shorter proximal shaft on the first dorsal proximal-middle radial that does not extend very far into the second interneural space. The anterior plate-like extension of the proximal-middle shaft in these two genera partially fits between the bifurcate tip of the first neural spine. *Diplospinus* and *Paradiplospinus* also have a proximal shaft on the first dorsal pterygiophore, which sits above the first and second interneural spaces, but the first neural spine is not bifurcate. The first neural spine of *Nesiarchus* is fused. The proximal shaft of the first dorsal pterygiophore is long in both *Gempylus* and *Nesiarchus*. In *Nesiarchus* it fits primarily in the second interneural space, but in *Gempylus* it extends above both the first and the second interneural spaces.

Character 52. In *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*, a plate-like ossification at the anteroventral corner between the proximal and distal portions of the proximal radials bears a small foramen. This foramen is absent or extremely reduced in the proximal radials of the other trichiurids and the outgroups.

Anal Fin

The morphology of the anal-fin pterygiophores in the outgroups and most of the trichiurids is identical to that described for the dorsal-fin pterygiophores.

Character 53. The first anal pterygiophore in the outgroups bears two well-developed supernumerary spines (Fig. 23A, B). *Aphanopus*, *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* bear two supernumerary spinous elements on the first anal pterygiophore (Fig. 23C–E, G, H). The first

supernumerary spine in these taxa is extremely reduced in size. Nakamura and Parin (1993) and Senta (1975) described the presence of two spines in the anal fin of *Tentoriceps*. However, in all the cleared and stained and alcohol-preserved specimens of *Tentoriceps* analyzed, I only found a single scale-like supernumerary element (Fig. 23J). *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* also have a single supernumerary element on the first anal pterygiophore. In the outgroups, the third fin-ray element associated with the first anal pterygiophore appears spinous in nature. The base of this element is completely or almost completely fused, forming a central foramen that accepts the posterior tip of the distal radial in *Gempylus* and *Nesiarchus*. However, this fin-ray element is bilaterally divided. *Diplospinus* and *Paradiplospinus* also have a third fin-ray element that is bilaterally divided, but the distal radial of the first anal pterygiophore does not pass through the central foramen. The distal radial of the first anal pterygiophore, which is in close association to the third fin-ray element, appears as a single ossification. The third fin-ray element of the first anal pterygiophore in the trichiurids is extremely reduced in size. In some specimens only one or two extremely reduced scale-like elements remain, and they appear to be remnants of a soft ray.

The two supernumerary spines of the first anal pterygiophore in *Gempylus* and *Nesiarchus* are well developed and rounded in cross section, except at their base, which embraces the articular facet of the first proximal-middle radial. The first supernumerary spine is longer than the second in *Nesiarchus*, whereas the rest of the outgroups have a longer second supernumerary spine. The supernumerary spines of the first anal pterygiophore of *Diplospinus* and *Paradiplospinus* are well developed, but V-shaped in cross section and bearing lateral wings. The first supernumerary spine of *Aphanopus*, *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* is extremely reduced. The second supernumerary spine of *Aphanopus* is elongate, triangular in ventral view, and slightly V-shaped in cross section. The supernumerary elements of the first anal pterygiophore in *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus* are modified and scale-like. The second supernumerary element is variable in shape, but it appears cardiform, or triangular, in ventral view, with well-developed lateral wings and V-shaped cross section.

The single scale-like supernumerary element of the first anal pterygiophore in *Tentoriceps* is similar to the second supernumerary elements of *Assurger*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus*. In *Eupleurogrammus*, the single supernumerary element is scale-like and bears lateral wings, but it is extremely reduced in size (Fig. 23F). The single supernumerary element in *Lepturacanthus* and *Trichiurus* is spinous in appearance (Fig. 23I, K) but triangular in cross section. This spine is much longer in *Lepturacanthus* than in *Trichiurus*, and this

feature was used by Nakamura and Parin (1993) as a character to differentiate these two genera.

The morphology of the posterior supernumerary element of the first anal-fin pterygiophore could be treated as a multistate character. However, the condition at the outgroup node is equivocal and the character is variable and difficult to categorize objectively. This potential multistate character must await a study that includes the gempylids and trichiurids together.

Benthodesmus is unique in that the first anal pterygiophore is abdominal in position, being located under the precaudal vertebrae. In all the outgroups and the rest of the trichiurids, the first anal pterygiophore articulates with the haemal spine of the first (or one of the first) caudal vertebrae.

The first anal pterygiophore of all the trichiurids, except *Benthodesmus*, and of the outgroups bears an elongate proximal shaft on the proximal-middle radial that articulates with its corresponding haemal spine. *Benthodesmus elongatus* and *B. simonyi* lack a proximal shaft on the first pterygiophore. However, the specimen of *B. tenuis* analyzed in this study has two poorly ossified proximal shafts that do not articulate with the vertebral column. The presence or absence of a proximal shaft in the first anal pterygiophore might prove to be a phylogenetically informative character within the genus *Benthodesmus*. However, its incorporation into a phylogenetic analysis must await the inclusion of most or all of the species of this genus in future studies. All of the trichiurids and the outgroups, except *Gempylus*, have a short anterior process on the first anal pterygiophore. *Gempylus* is unique in that the anterior process is extremely elongate and is almost equal in length to the proximal shaft.

Radiographs of the holotype of *Evoxymetopon taeniatum* show hyperostosis of some of the anal-fin proximal-middle radials.

Character 54. All the outgroups and the trichiurids *Aphanopus* and *Benthodesmus* have true soft rays (i.e., bilaterally divided, segmented, and distally branched) throughout the whole length of the anal fin (Fig. 24A, B). In *Assurger*, *Lepidopus*, and *Evoxymetopon*, most of the anal-fin rays are extremely reduced; only the last few rays are external, can be identified as true soft rays, and are connected by a membrane. In *Aphanopus* and some species of *Benthodesmus*, the anal fin is composed of true external soft rays that are united by a membrane along its entire length. However, one must be cautious in the interpretation of this character because its condition appears to be dependent on the size of the specimens. In this study, the cleared and stained specimens of *Lepidopus* have well-developed soft rays throughout the anal fin but only the posterior ones are connected by a membrane. Larger dry-skeletal preparations of this taxon show an extreme reduction of these anterior fin rays. In *Lepturacanthus* and *Trichiurus*, the anal-fin soft rays are reduced to spinule-like processes that are not branched or segmented (Fig. 24E). These spinules

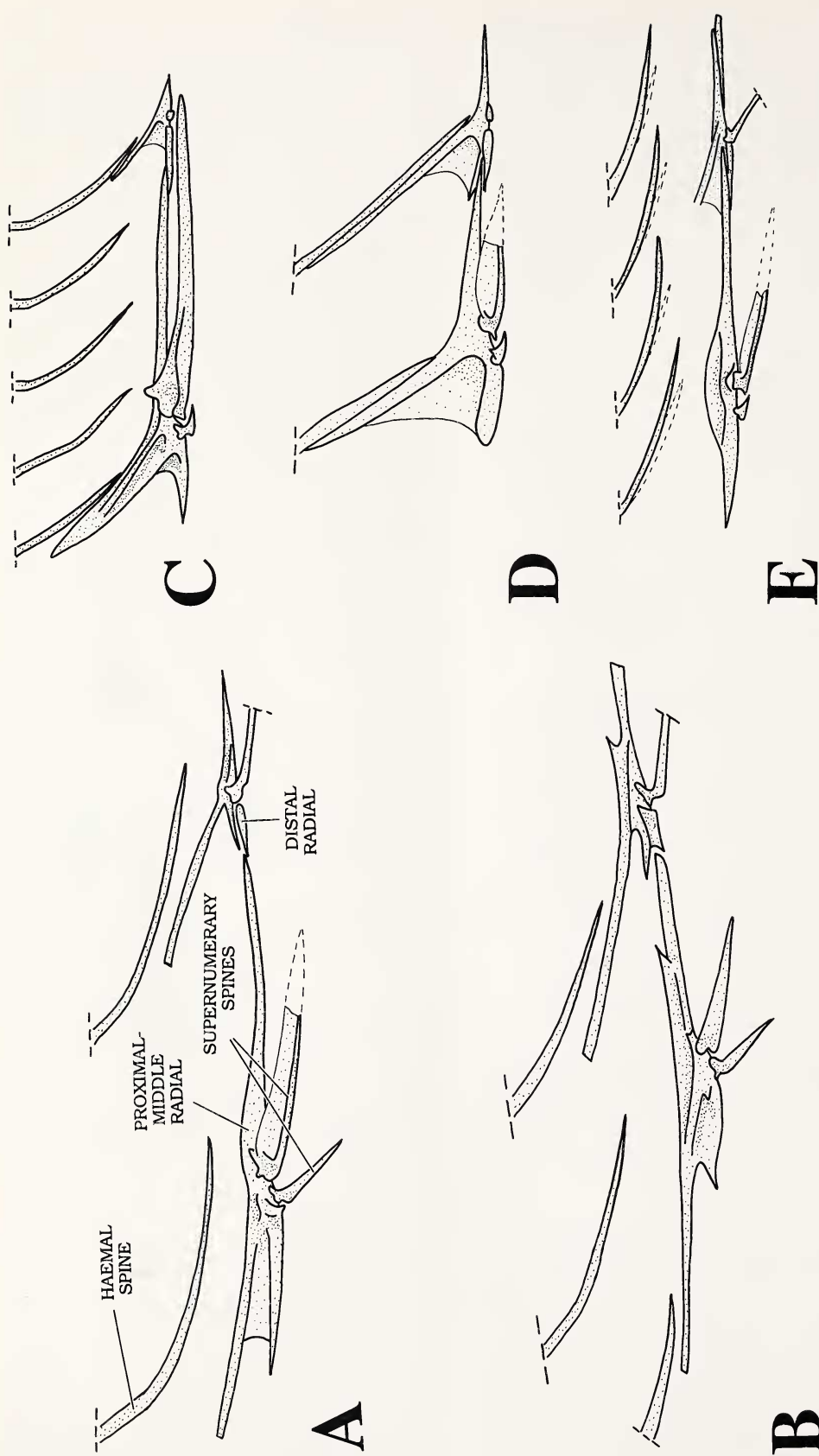


Figure 23. A-E. Left view of the first and second anal-fin pterygiophores: (A) *Diplospinus multisriatus*; (B) *Paradiplospinus antarcticus*; (C) *Aphanopus carbo*; (D) *Assurger anzac*; (E) *Benthodesmus elongatus*.

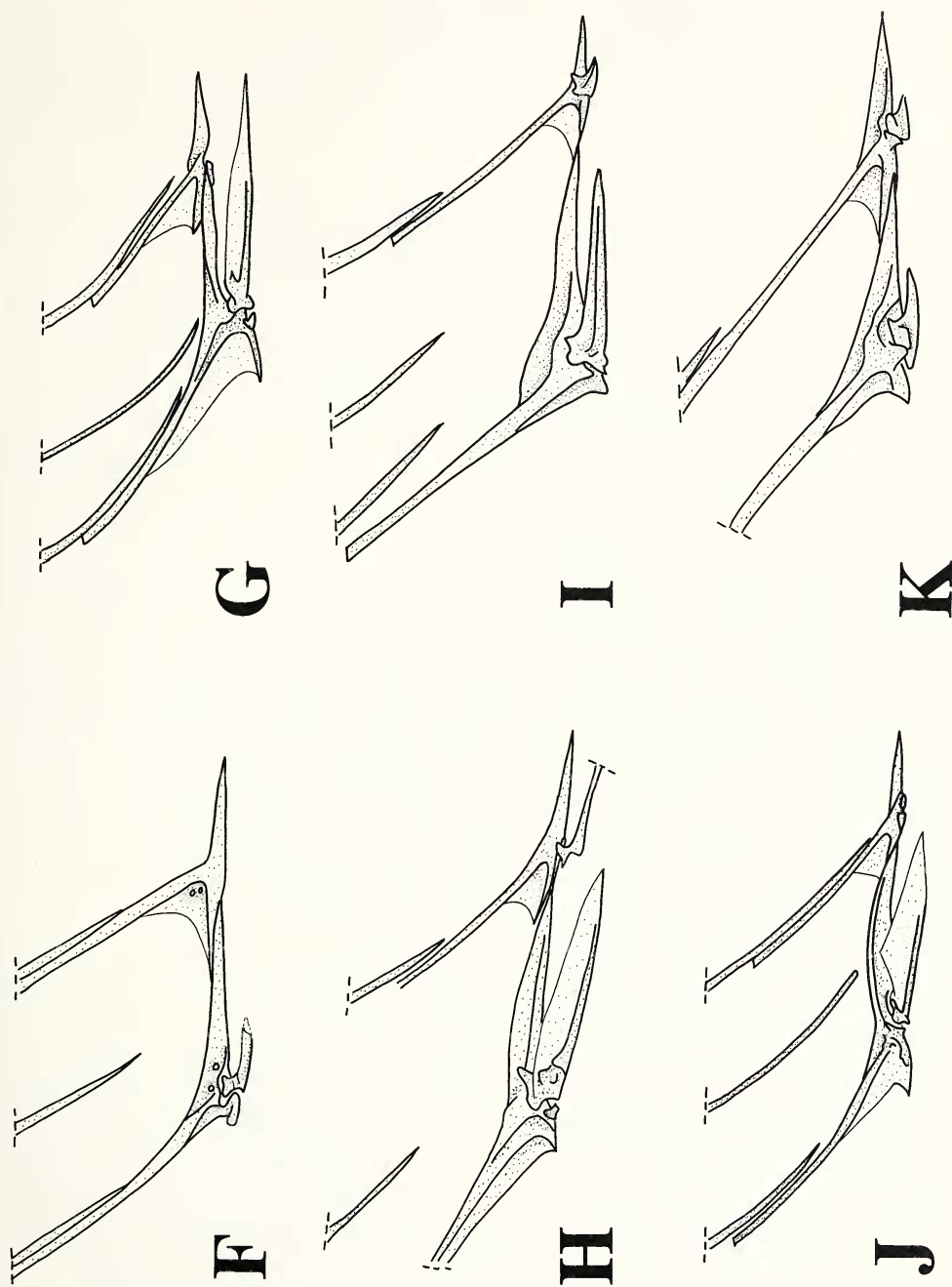


Figure 23. F-K. Left view of the first and second anal-fin pterygiophores: (F) *Evoxymetopon taeniatus*; (G) *Eupleurogrammus glossodon*; (H) *Lepidopus fitchii*; (I) *Lepturacanthus savala*; (J) *Tentoriceps cristatus*; (K) *Trichiurus lepturus*.

are V-shaped in cross section and resemble the morphology of the supernumerary spine of the first anal pterygiophore.

Tentoriceps shares the same condition as *Lepturacanthus* and *Trichiurus*, but the rays are reduced to minuscule scale-like elements that do not penetrate the skin externally (Fig. 24D). *Eupleurogrammus* shows another derived condition in which the rays barely penetrate the skin and appear as small fused knobs on the proximal-middle radials (Fig. 24C).

Character 55. The anal-fin pterygiophores of the outgroups are characterized by the presence of proximal-middle and distal radials (Fig. 24A). Trichiurids, except *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*, have an anal fin in which the pterygiophores of the soft ray portion are composed of proximal, middle, and distal radials (proximal-middle and extra distal of Johnson, 1986; Fig. 24B). *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus* are characterized by the fusion of the radials as a single unit (Fig. 24C–D).

CAUDAL COMPLEX

The caudal complex is composed of a series of caudal rays and supporting bones (Fig. 25).

Character 56. All the gempylids are characterized by the presence of a well-developed caudal complex. In some of the trichiurids, the caudal fin complex has become reduced or completely lost (Fig. 26). Senta (1975) briefly described the presence of an extremely reduced internal caudal complex in *Tentoriceps*. The posterior tip of the body in *Tentoriceps* is more rounded in appearance than those of *Lepturacanthus* and *Trichiurus*, which bear extremely pointed caudal tips. Internally, *Tentoriceps* bears two rudimentary hypural plates on the last vertebral element. From 6 to 14 rudimentary rays are also present in the cleared and stained specimens of *Tentoriceps* analyzed in this study. These rays barely penetrate the skin and articulate mainly on the margins of the reduced hypural plate and the dorsal surface of the last vertebral element. Adults of *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* are characterized by the complete absence of a caudal complex.

Character 57. All outgroups and those trichiurids with a well-developed caudal skeleton bear an ultimate centrum that has undergone flexion and forms a urostyle. In *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*, the last vertebral centrum has not undergone flexion. In *Lepturacanthus* and *Trichiurus*, the posterior tip of the body is pointed, and the last vertebral element bears an extremely reduced neural process and a haemal spine that is branched distally in some specimens. The last vertebral element of *Eupleurogrammus* also bears an extremely reduced neural process. However, the haemal spine of this last verte-

bral element is spatulate and supports the more rounded tail of this genus.

The following descriptions refer only to those trichiurids and outgroups that bear a well-developed caudal complex, unless noted otherwise.

Caudal-fin Rays

The caudal rays are divided into principal and procurent rays. The principal caudal rays are usually branched and more elongate and articulate with the upper and lower hypural plates, including the parhypural (Dunn, 1983). The procurent rays are usually unbranched and articulate with the neural or haemal elements of the preural centra. Collette et al. (1984) tabulated the meristic differences of caudal fin rays among the scombroids. All scombroids bear a 9+8 pattern of principal caudal rays on the dorsal and ventral hypural plates, respectively. However, a slight meristic difference appears in the numbers of procurent rays among the major scombroid groups. Trichiurids are characterized by having 6 or 7 dorsal and ventral procurent rays. All gempylids, except *Diplospinus* and *Paradiplospinus*, have between 8 and 11 procurent rays dorsally and ventrally. *Diplospinus* and *Paradiplospinus* are similar to the trichiurids in that they bear 4 or 5 and 5 or 6 procurent rays dorsally and ventrally, respectively. Scombrids have between 10 and 17 dorsal and 10 and 18 ventral procurent rays, whereas billfishes bear between 8 and 13 and 11 and 13, respectively. Although there is a reduction in the number of procurent rays in the trichiurids, the character is not used in the analysis because of the subjectivity in the determination of possible character states. Collette and Chao (1975) noted that in trichiurids and gempylids the bases of the caudal-fin rays extend only partly onto the hypural plate. In contrast, scombrids are characterized by having caudal-fin ray bases that cover the hypural plates almost completely.

Epurals

The epurals are median bones located between the neural spine of preural centrum 2 and the upper hypural plate.

Character 58. All trichiurids have a single epural. *Diplospinus* and *Paradiplospinus* are characterized by the presence of two epurals, whereas *Gempylus* and *Nesiarchus* have three. Russo (1983) noted that all gempylids, except *Diplospinus* and *Paradiplospinus*, have three epurals. Although the condition for this character in this study appears to be equivocal at the outgroup node, I consider the plesiomorphic condition to be that present in most gempylids (i.e., presence of three epurals).

Uroneurals

Uroneurals are paired bones located anterodorsally above the urostyle. The uroneurals represent the modified neural arches of the first preural and ural centra.

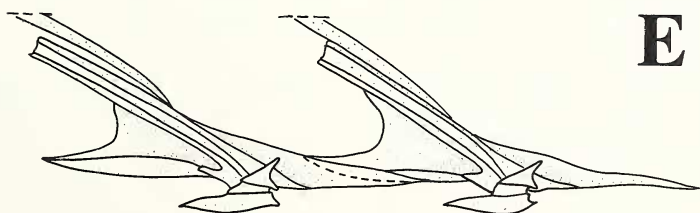
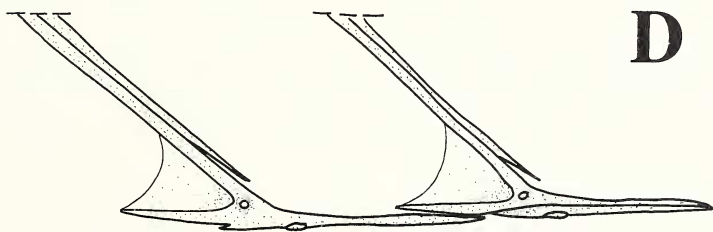
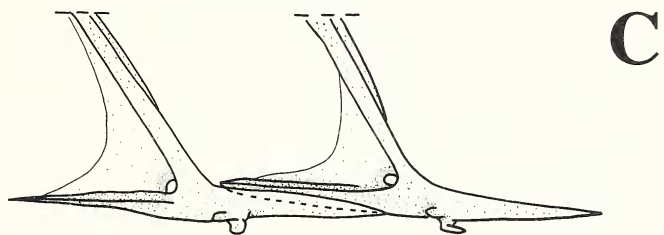
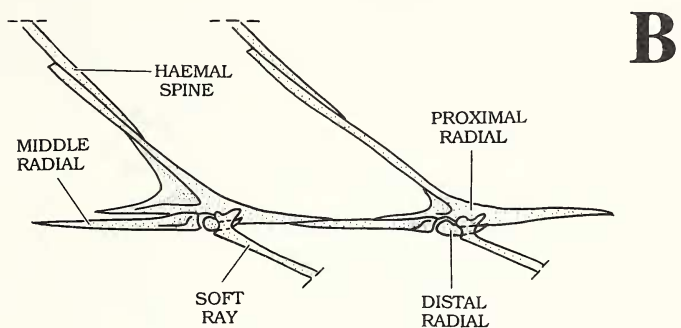
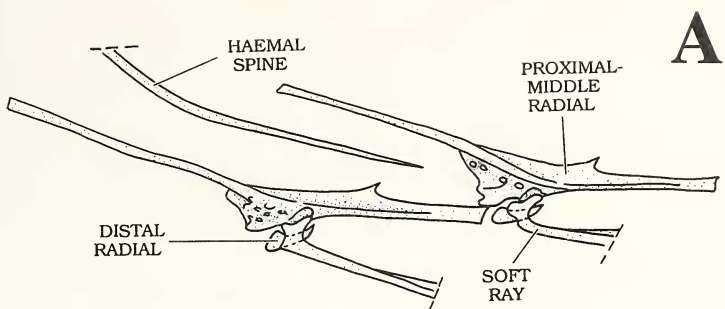


Figure 24. Left lateral view of two anal-fin pterygiophores and soft rays: (A) *Paradiplospinus antarcticus*; (B) *Aphanopus carbo*; (C) *Eupleurogrammus glossodon*; (D) *Tentoriceps cristatus*; (E) *Trichiurus lepturus*.

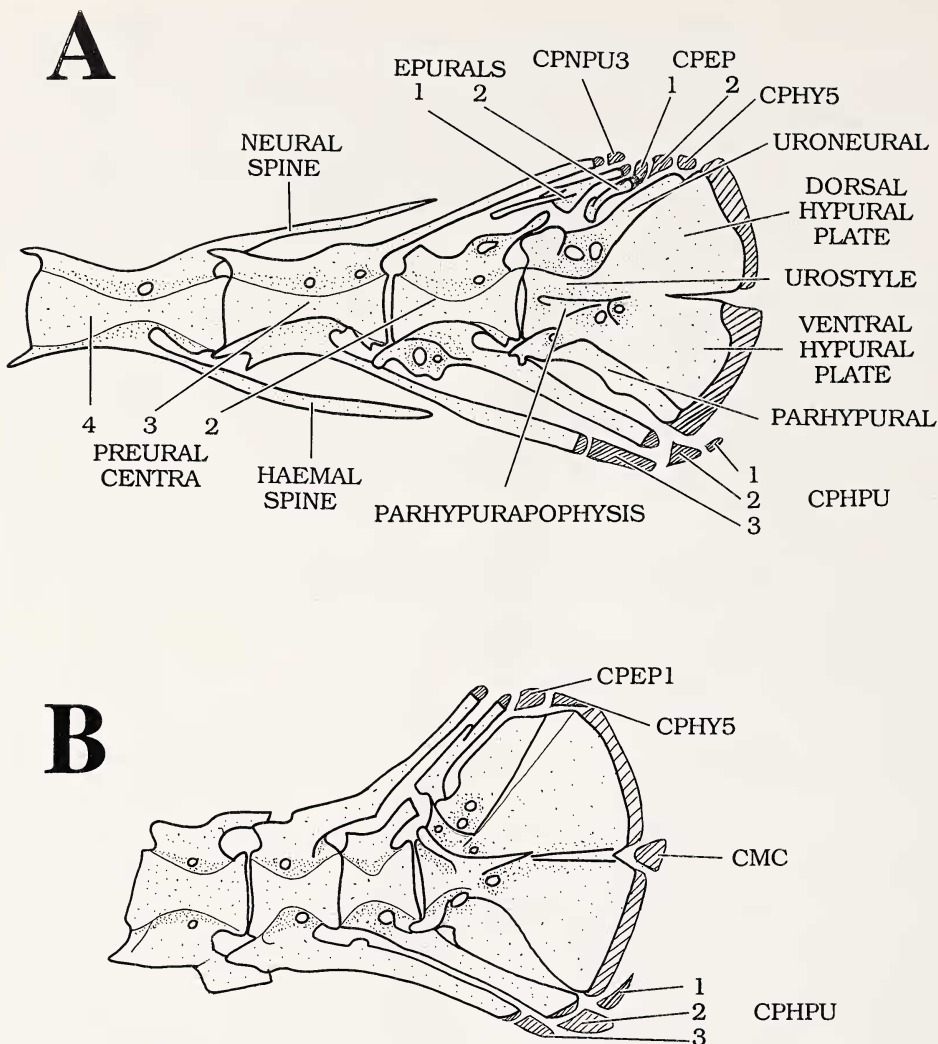


Figure 25. Left lateral view of the caudal-fin skeleton (fin rays not included; cartilaginous elements striped; CPNPU3, postneural spine cartilage of preural centrum 3; CPEP, postepural cartilages; CPHY5, posthypural cartilage of hypural 5; CMC, median caudal cartilage; CPHPU, parhypural and haemal spine cartilages of preural centra): (A) *Paradiplospinus antarcticus*; (B) *Assurger anzac*.

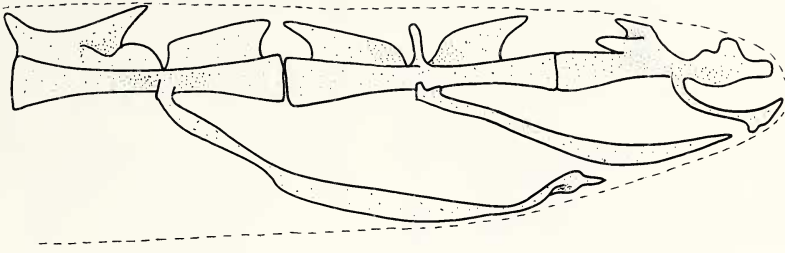
All trichiurids and the outgroups *Diplospinus*, *Gempylus*, and *Paradiplospinus* have a single uroneural. *Nesiarchus* has two uroneurals. Russo (1983) considered the fusion of the uroneurals with the urostyle in *Diplospinus*, *Gempylus*, and *Paradiplospinus* to be a synapomorphy uniting these three genera. Fujita (1990) reported that the uroneural of *Diplospinus* is fused to the urostyle and the upper hypural plate but concluded that the urostyle of *Gempylus* is autogenous. In this study, I also note that the uroneurals of *Paradiplospinus* and all the trichiurids with a well-developed caudal fin complex are fused, except in *Aphanopus* and *Benthodesmus*. In these two trichiurids, the uroneural is closely associated with the urostyle, but a joint between these two bones is visible. The degree

of fusion of the uroneurals to the urostyle and upper hypural is excluded from this analysis because the condition appears to be quite variable and dependent on the size and degree of ossification of the specimens and is difficult to interpret.

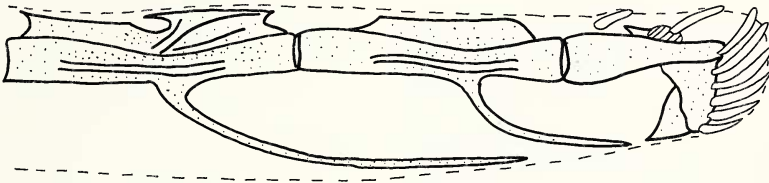
Preural Centra

The preural centra discussed in this study include the three posterior-most vertebral elements, excluding the urostyle. They bear well-developed haemal and neural arches and spines. These elements are numbered from posterior to anterior, starting anteriorly to the urostyle, as preural centra 2, 3, and 4. In the trichiurids and outgroups, preural centra 2 and 3 bear well-developed haemal spines that

A



B



C

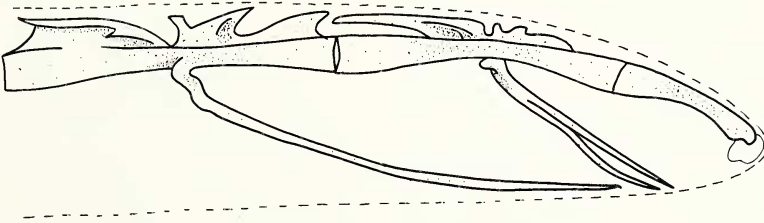


Figure 26. Left lateral view of the caudal tip (cartilaginous elements striped): (A) *Eupleurogrammus glossodon*; (B) *Tentoriceps cristatus*; (C) *Trichiurus lepturus*.

support the ventral procurent rays. In addition, preural centrum 3 of the trichiurids bears a well-developed neural spine that supports some of the dorsal procurent rays.

In trichiurids, the haemal spines of preural vertebrae 2 and 3 are fused to their respective centra. The haemal spines of preural centra 2 and 3 in the outgroups are usually autogenous. However, in a large specimen of *Paradiplospinus*, the haemal spine of the preural centrum 3 appeared to be fused. In his phylogenetic analysis of the gempylids, Russo (1983) noted that all gempylids, except *Dip-*

lospinus and *Paradiplospinus*, bear preural centra with fused haemal spines. He considered the presence of an autogenous haemal spine on preural centrum 2 to be a synapomorphy uniting these two genera. The degree of fusion of the haemal spines to their respective preural centra varies with size, is dependent on the degree of ossification of the specimens, and is difficult to interpret. In scombroids preural centrum 2 lacks a neural spine (Russo, 1983).

Character 59. In trichiurids, preural centrum 4 is characterized by the presence of shortened haemal

and neural spines which do not extend well past the anterior margin of preural centrum 3. The outgroups are characterized by the presence of haemal and neural spines on preural centrum 4 that are long and extend past, or as far as, the posterior margin of preural centrum 3.

Urostyle

The urostyle supports the parhypural and the dorsal and ventral hypural plates posteriorly and the uroneural anterodorsally. The morphology of the urostyle is similar among the taxa analyzed in this study.

Parhypural

The parhypural is a median bone located ventral to the urostyle and anteroventral to the ventral hypural plate. The parhypural is considered to be the modified haemal spine of the first preural centrum. It bears the last haemal arch that is traversed by the dorsal aorta. The parhypural bears a longitudinal lateral shelf or parhypurapophysis. Fujita (1990) noted that the parhypural is autogenous in all the gempylid taxa that he analyzed, except *Diplospinus*, where the parhypural is fused to the urostyle and the ventral hypural plate. *Gempylus* and *Nesiarchus* share the condition described by Fujita (1990) for the rest of the gempylids. Russo (1983) indicated that the parhypural of *Gempylus* is closely associated with the ventral hypural plate, but a distinct joint can be seen between them. Fujita (1990: table 2-20) indicated that *Benthodesmus elongatus pacificus* Parin and Becker 1970 (= *B. pacificus*) is characterized by a parhypural that is completely fused to the ventral hypural plate. However, in his illustrations, Fujita (1990: fig. 522) depicted a clear border between the parhypural and the ventral hypural plate. All of the specimens of *Diplospinus* and the trichiurids analyzed in this study share the presence of a fused parhypural. A small specimen of *Paradiplospinus* was characterized by the presence of an autogenous parhypural, whereas larger specimens had fused parhypurals. Russo (1983) also indicated that a joint is present distally between the parhypural and the ventral hypural plate of *Paradiplospinus*. The degree of fusion between the parhypural and the ventral hypural plate is variable among the gempylids and dependent on the degree of ossification of the specimens.

Hypurals

The hypurals are a series of five median bones that are subtriangular in shape and articulate or are fused to the posterior margin of the urostyle. The hypurals are fused into two or more units or plates that support the bases of the principal caudal-fin rays.

Character 60. Russo (1983) considered the pattern of fusion among the hypurals as two charac-

ters. In his character 79, Russo (1983) concluded that the presence of separate third, fourth, and fifth hypurals represents the plesiomorphic condition; the fusions of the third and fourth or the third, fourth, and fifth represent the apomorphic conditions. Furthermore, in his character 81, Russo (1983) considered the separation of the first and second hypurals as the plesiomorphic condition and their fusion as the apomorphic condition. All trichiurids, plus the outgroups *Diplospinus* and *Paradiplospinus*, have a ventral and a dorsal hypural plate formed by the fusion of the first and second and the third, fourth, and fifth hypurals, respectively. In *Gempylus*, the dorsal and ventral hypural plates are formed by the fusions of the first and second and the third and fourth hypurals, respectively. The fifth hypural of *Gempylus* is closely associated with the fourth hypural and the urostyle, but a distinct joint is present between these bones. In *Nesiarchus*, all hypurals are separate. The degree of fusion of these elements is dependent on the size of the specimens. Although this character should be interpreted with caution, I include it in the analysis as a single multistate character that combines the conditions of the ventral and dorsal hypural plates described by Russo (1983). The condition of this character at the outgroup node is equivocal. However, I agree with Russo's (1983) analysis and consider the plesiomorphic condition to be that in which all the hypurals are free (i.e., the hypural plates formula is I + II + III + IV + V). The apomorphic conditions are the presence of three hypural plates (i.e., I-II + II-IV + V) or two hypural plates (i.e., I-II + III-IV-V).

Character 61. The ventral and dorsal hypural plates of the trichiurids and the gempylids *Diplospinus* and *Paradiplospinus* are fused longitudinally, except distally at their corners. Thus, the posterior margin of the hypural plates forms a notch (hypural notch of Russo, 1983). Russo (1983: character 80) concluded that the presence of a small hypural notch represents a synapomorphy uniting *Diplospinus* and *Paradiplospinus*. The trichiurids share this condition. The plesiomorphic condition is that present in the rest of the gempylids, which bear a large hypural notch.

Cartilaginous Elements

Fujita (1990) described the cartilaginous elements of the caudal fin complex of several scombroids, including the trichiurid *Benthodesmus elongatus pacificus* (= *B. pacificus*) and the gempylids *Diplospinus multistriatus*, *Nealotus tripes* Johnson 1865, *Neopinnula orientalis* (Gilchrist and von Bonde 1924), *Nesiarchus nasutus*, *Promethichthys prometheus* (Cuvier in Cuvier and Valenciennes 1832), and *Ruvettus pretiosus* Cocco 1829.

All trichiurids and outgroups bear a single posthypural cartilage at the posterior tip of the fifth hypural (CPHY5 of Fujita, 1990). Trichiurids and the outgroups, except *Diplospinus* and *Paradiplo-*

spinus, have a single post-epural cartilaginous element (CPEP of Fujita, 1990). In trichiurids this post-epural cartilaginous element is associated with the single epural bone of these taxa (CPEP1). In contrast, the single post-epural element of the outgroups, excluding *Diplospinus* and *Paradiplospinus*, is associated with the third epural bone of these taxa (CPEP3). *Diplospinus* and *Paradiplospinus* are characterized by the presence of two separate post-epural cartilages (CPEP1 and 2 of Fujita, 1990) associated with the two epurals in their caudal skeleton. A cleared and stained specimen of *Paradiplospinus antarcticus* in this study shows a single post-epural cartilage. However, upon close examination through transmitted light, one can discern the presence of two darker blue cartilaginous centers within this single unit.

All of the trichiurids bear three posthaemal spine cartilaginous elements distally on the parhypural and the haemal spines of preural centra 2 and 3 (CPHPU1, 2 and 3 of Fujita, 1990). *Diplospinus*, *Gempylus*, and *Paradiplospinus* share this condition with the trichiurids. Fujita (1990) noted that *Nesiarchus* and all of the other gempylids, except *Diplospinus*, plus the three species of scombrids in his study have two posthaemal spine cartilages.

Character 62. All of the trichiurids with a well-developed caudal fin have a median caudal cartilage (CMC of Fujita, 1990). This single cartilaginous block lies slightly posterior to the hypural notch formed by the upper and lower hypural plates. All the outgroups lack this element.

Character 63. All of the outgroups bear a cartilaginous postneural spine element on the third preural vertebra (CPNPU3 of Fujita, 1990). The third postneural spine cartilage is absent in all trichiurids.

OTOLITH MORPHOLOGY

Otolith features are depicted in Figure 27. The medial face of the sagittae is characterized by the presence of a longitudinal groove, the sulcus, which is usually divided into an anterior ostium and a posterior cauda. The ostium usually opens anteriorly through the excisura, which may or may not be bordered by a rostrum and an antirostrum. If present, a postcaudal trough marks the opening of the cauda. The dorsal and ventral borders of the sulcus are delimited by longitudinal ridges called the cristae superior and inferior, respectively.

The outgroup genera *Gempylus* and *Nesiarchus* (Fig. 28B, C) have very similar otolith morphologies. The sagittae have extremely elongate rostra and well-defined antirostra; an extremely shallow sulcus that opens both posteriorly and anteriorly; reduced, nonoverhanging cristae superior and inferior. The only difference between the sagittae of these two genera seems to be the presence of a notch in the posterior margin of the otolith and a shorter antirostrum in *Nesiarchus nasutus*. However, the variability of these characters cannot be

evaluated since only a single drawing of the otolith of *Nesiarchus* was available for comparison.

Diplospinus, *Paradiplospinus*, and all the trichiurids analyzed in this study, except *Lepidopus fitchi* (Fig. 28I), have sagittae with a sulcus that lacks a postcaudal trough. On the other hand, the sagittae of *Gempylus* and *Nesiarchus* show a very shallow sulcus that is open posteriorly. Other scombroids analyzed (e.g., basal gempylids and billfishes) have sagittae with a wide postcaudal trough or a sulcus with a wide, fan-shaped posterior margin (e.g., some scombrids). The latter group, even though they have a continuous posterior margin, could still be considered as open because of the extreme fan shape of the posterior margin of the cauda. Frost (1928) described the sagittal otoliths of *Lepidopus caudatus* as having a narrow postcaudal trough. A description and drawing of a sagitta of *L. caudatus* by Demestre et al. (1993) does not show a postcaudal trough. The 20 sagittae of this species analyzed in this study do not have a postcaudal trough (Fig. 28H). If the sagittae of some specimens of *L. caudatus* have a postcaudal trough, it may be very uncommon. Fitch and Gotshall (1972) included a photograph of a sagitta of *Lepidopus xantusi* Goode and Bean 1895 (= *L. fitchi*) that clearly shows a posterior opening of the sulcus. The same condition was found in most of the 42 sagittae of this species analyzed.

Anderson and Cailliet (1975) noted that the otolith morphology of their specimen of *Benthodesmus elongatus pacificus* (= *B. pacificus*) differs from that described by Fitch and Gotshall (1972) in the presence of a reduced antirostrum and a more rounded ventral surface with the greatest height occurring along the middle third of the longitudinal axis. Although they acknowledge that the specimens had been preserved in formalin prior to examination of the sagittae, the morphology is clearly distinct. In Anderson and Cailliet (1975; fig. 2) it appears that the sulcus extends along the whole medial face and opens both posteriorly and anteriorly. The well-developed sulcus and the elongate rostrum are in contrast with the sagitta of *B. pacificus* analyzed in this study (Fig. 28G).

Reduced ornamentation of the ventral margins of the otoliths is characteristic of *Diplospinus*, *Gempylus*, *Paradiplospinus*, and all the trichiurids in this study, except *Lepidopus*, *Lepturacanthus*, and *Trichiurus*. *Diplospinus* seems to have some slight ornamentation on the ventral margin, but its condition is not comparable to the strongly serrate and irregular ventral margins that characterize *Nesiarchus*, *Lepidopus*, *Lepturacanthus*, *Trichiurus*, and most scombroids. However, the degree of ornamentation seems to be quite variable within species. For example, large sagittae of *Gempylus* appear to have little ornamentation, whereas smaller sagittae are heavily ornamented.

Diplospinus, *Paradiplospinus*, and all the trichiurids have sagittae with reduced ornamentation on their dorsal margins. All other scombroid genera

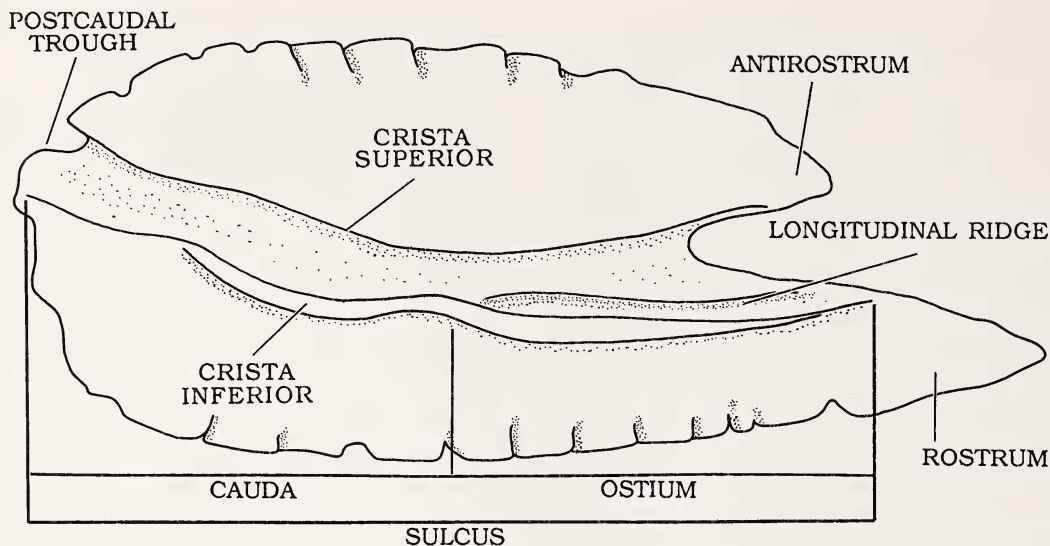


Figure 27. Generalized diagram of the medial face of a left sagitta from a hypothetical trichiurid.

analyzed have sagittae with strong ornamentation in the form of irregular, serrate dorsal margins. Some of the otoliths of *Diplospinus* and *Paradiplospinus* have a slightly ornamented dorsal margin. However, this is not comparable to the plesiomorphic condition present in *Gempylus* and *Nesiarchus*. Again, the ornamentation appears to be variable through ontogeny.

A possible autapomorphy for the genus *Assurger* is the presence of a tapering posterior end that turns abruptly downward forming a posteroventral dome (Fig. 28F), which is absent or reduced in the other genera studied. However, this possible character is not included in the data matrix because its variability could not be determined since only three otoliths (i.e., two individuals) of *Assurger* were available.

Character 64. *Diplospinus* and *Paradiplospinus* (Fig. 28A, D), plus the trichiurids *Aphanopus* and *Benthodesmus* (Fig. 28E, G), have poorly developed rostra and antirostra. Fitch and Gotshall (1972) described the sagittae of *Aphanopus* as lacking a rostrum. *Gempylus* and *Nesiarchus*, the rest of the trichiurids, and the other scombroid genera analyzed in this study have well-developed rostra and antirostra. Although the condition for this character at the outgroup node of this study is equivocal, the presence of well-developed rostra and antirostra is considered to be the ancestral condition since it is present in the rest of the scombroids analyzed outside of the trichiurids and the outgroups *Diplospinus* and *Paradiplospinus*. This character, however, is variable and should be interpreted with caution. *Gempylus* and *Nesiarchus* have an extremely elongate rostrum, whereas *Assurger*, *Lepidopus*, *Lepturacanthus*, and *Trichiurus*

possess a well-developed rostrum and antirostrum that is not nearly as elongate.

Character 65. The presence of overhanging cristae inferior and superior characterizes the genera *Aphanopus*, *Assurger*, *Lepidopus*, *Lepturacanthus*, and *Trichiurus*. All the other trichiurids and outgroups lack the presence of overhanging cristae.

Character 66. *Lepturacanthus* and *Trichiurus* (Fig. 28J, K) share the presence of a longitudinal ridge on the ostium. The longitudinal division of the ostium by a ridge was already noted by Frost (1928) in the sagittae of *Trichiurus*. The otoliths of *Lepturacanthus* have not been previously described. The otolith morphology of *Lepturacanthus* is extremely similar to that of *Trichiurus*. The rest of the trichiurids and outgroups lack a longitudinal ridge on the ostium.

DISCUSSION

Analysis of the data matrix supports some of the previously proposed hypotheses of relationships within the trichiurid fishes. Among these hypotheses are: the monophyly of the trichiurids; the monophyly of *Diplospinus* and *Paradiplospinus* and their sister group relationship to the trichiurids; the close relationships of the trichiurids *Lepturacanthus* and *Trichiurus*; and the basal position within the cutlassfishes of *Aphanopus* and *Benthodesmus*.

Johnson (1986) proposed a monophyletic Trichiurinae (trichiurids of this study) based on nine synapomorphies. The present study includes four of these nine synapomorphies and increases the support for his hypothesis by adding 17 more (Fig. 4).

The sister group relationship of *Diplospinus*-*Paradiplospinus* to the trichiurids (Fig. 4) agrees

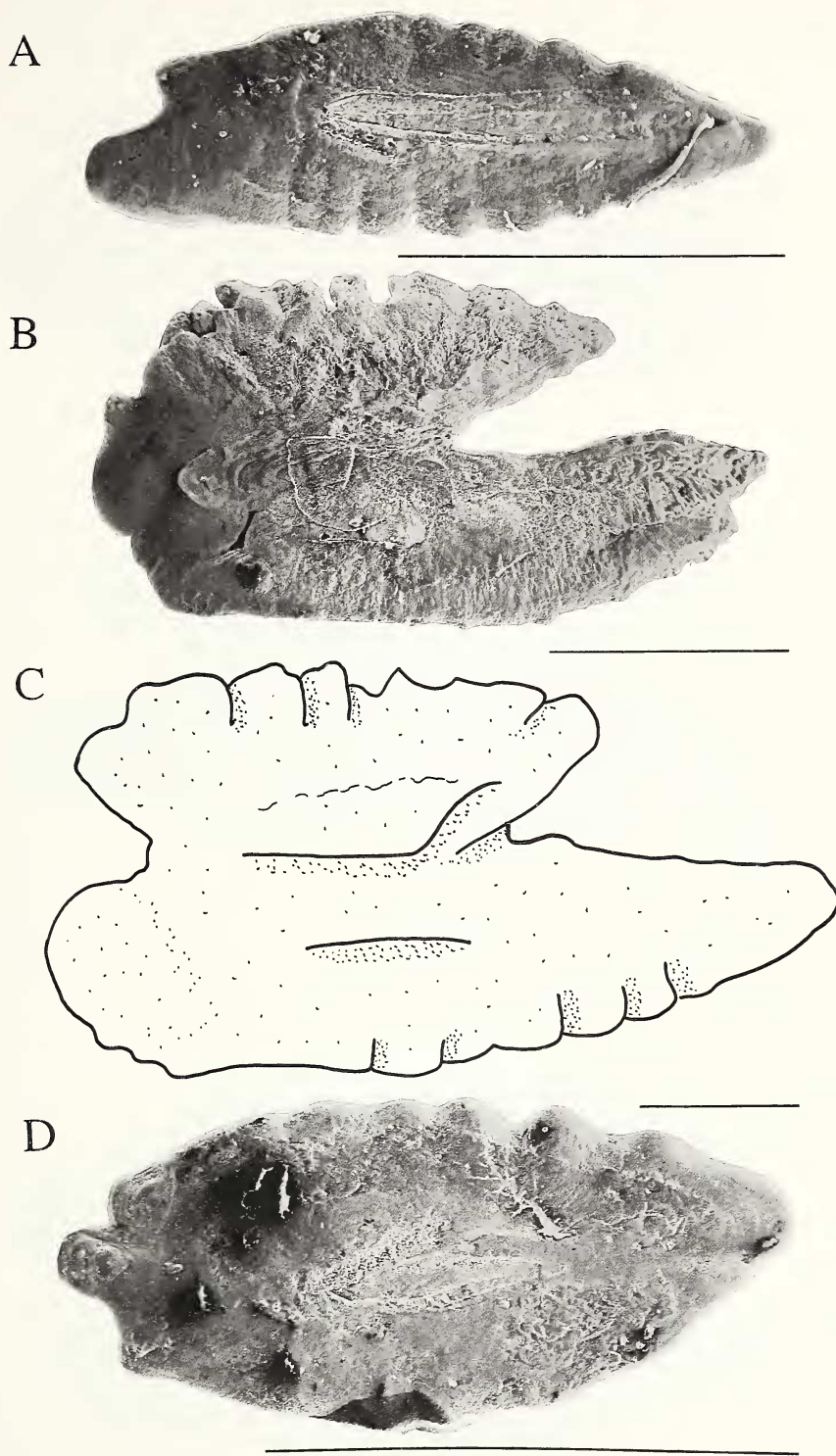
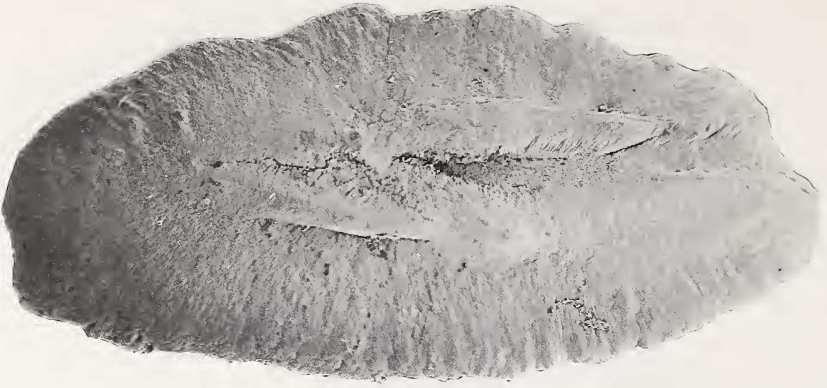


Figure 28. A–D. Electron microscopy photographs and line drawing (scale bar = 2 mm) of the medial face of the left sagittae of: (A) *Diplospinus multistriatus*; (B) *Gempylus serpens*; (C) *Nesiarchus nasutus* (provided by Dr. D. Nolf); (D) *Paradiplospinus antarcticus*.

E



F



G

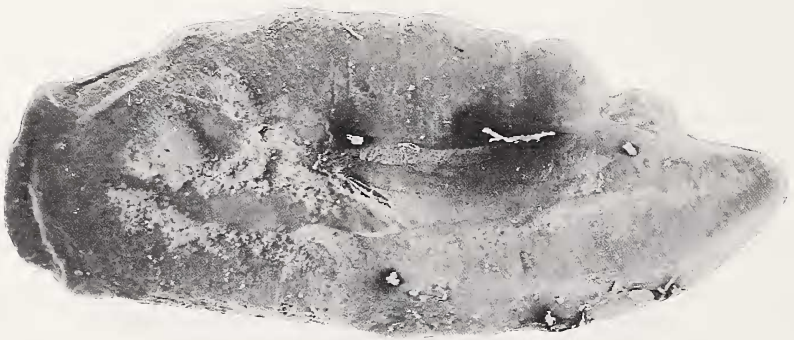


Figure 28. E–G. Electron microscopy photographs and line drawing (scale bar = 2 mm) of the medial face of the left sagittae of: (E) *Aphanopus arigato*; (F) *Assurger anzac*; (G) *Benthodesmus pacificus*.

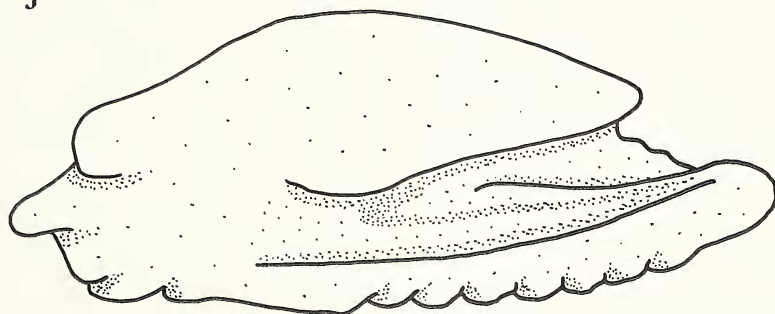
H



I



J



K



Figure 28. H-K. Electron microscopy photographs and line drawing (scale bar = 2 mm) of the medial face of the left sagittae of: (H) *Lepidopus caudatus*; (I) *Lepidopus fitchi*; (J) *Lepturacanthus savala*; (K) *Trichiurus lepturus*.

with the conclusion of Parin and Becker (1972), who also considered these gempylid genera as the closest relatives of the trichiurids. Previous to the work of Parin and Becker (1972), most authors included *Diplospinus* and *Paradiplospinus* within the Trichiuridae. Recently, Carpenter et al. (1995) presented the results of several analyses of relationships among the scombroids based on morphological characters. They analyzed a revised version of the data matrix of Johnson (1986), a combined data set from Collette et al. (1984) and Johnson (1986), and a data set in which the coding of one of Johnson's (1986) characters was changed. In all of their analyses, the clade including *Diplospinus* and *Paradiplospinus* appeared as the sister group of the trichiurids.

Diplospinus and *Paradiplospinus* are so similar in their osteology that they have been considered a single genus (Russo, 1983). In addition, Fitch and Gotshall (1972) questioned the validity of *Paradiplospinus*, indicating that the small differences in the sagittae of these two genera seem to be specific rather than generic in magnitude. However, in this study, one feature defines the species *P. antarcticus*: a posteriorly directed basibranchial attachment on the urohyal. According to Russo's (1983) hypothesis of gempylid relationships, this basibranchial attachment appears to have been lost once at the ancestral node separating *Lepidocybium* from remaining gempylids, to be regained independently in *Epinnula*, *Thyrsitoides*, and *Thyrsitops*. In addition, the distinct condition of the pelvic girdle, in which the external elements are absent and the basipterygium is well developed, also distinguishes this genus from the closely related *Diplospinus*.

The loss of external elements of the pelvic girdle has occurred twice independently within the trichiurids: in *Aphanopus* and the clade *Lepturacanthus-Trichiurus*. This conclusion is supported by the ontogenetic data of Gago (1997), which also showed that larvae of *Aphanopus* bear a well-developed pelvic girdle with external elements. The condition in *Aphanopus* is unique because the basipterygium is extremely reduced and consists of only a small ossification under the pectoral girdle. *Lepturacanthus* and *Trichiurus* lack all elements of the pelvic girdle. Remaining trichiurids have reduced pelvic girdles, but they still retain the external fin elements. Among the other gempylids, not analyzed in this study, *Promethichthys*, *Rexichthys* Parin and Astakhov 1987, and some species of *Rexea* have also lost the external pelvic-girdle elements (Nakamura and Parin, 1993). Following the hypothesis of gempylid relationships of Russo (1983), this loss of external pelvic-girdle elements appears to have occurred independently at least three times. However, Russo (1983) did not describe the pelvic girdle of gempylids. Thus, I have no evidence about the degree of reduction of the basipterygium among these genera.

In this study, monophyly of *Lepturacanthus* and

Trichiurus is defined by six synapomorphies, including two homoplasies (Fig. 4). Tucker (1956) included these two genera within the subfamily Trichiurinae Swainson 1839. In his tree, the Trichiurinae appears as emerging at the same node with his subfamily Lepidopodinae and a monophyletic group including *Aphanopus* and *Benthodesmus*. Furthermore, he questioned whether the subfamily Trichiurinae appeared as a descendant of his *Nesiarchus-Diplospinus* bridge or if it had an earlier divergence within the Gempylidae. Tucker (1956) indicated that, if further examination of the palatine of the gempylid *Thyrsitoides marleyi* Fowler 1929 indicated the presence of a villiform band of teeth, it could be considered as evidence for an earlier offshoot of the Trichiurinae. Matsubara and Iwai (1958) indicated the absence of teeth in *Mimasea* (= *Thyrsitoides*), whereas Russo (1983) described the presence of a single row of teeth on the ventral margin of the palatine of this species. Matsubara and Iwai (1958: 33) concluded that, because the presence of a number of small teeth on the palatine "is rather variable by the species, it appears likely that the palatine teeth are not so important [a] characteristic in considering the gempylid-trichiurid relationship," as assumed by Tucker (1956). Although Russo (1983) indicated that replacement teeth were present dorsomedially to the ventral row of teeth in his specimens of *Thyrsitoides marleyi*, the condition is not comparable to that in *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*. The specimens of these three genera analyzed in this study are characterized by the presence of a villiform band of small teeth that covers most of the length of the palatine.

Tucker (1956) also mentioned the presence of a concave free margin of the subopercle as a character that is present not only in *Lepturacanthus* and *Trichiurus* but also in some gempylids such as *Epinnula* and *Neopinnula*. Russo (1983) concluded that the apparent concave condition of the subopercle in the gempylids *Nealotus*, *Promethichthys*, *Rexea*, and *Ruwettus* is not comparable to that of the trichiurids. Furthermore, he noted that *Epinnula* and *Neopinnula* have a subopercle with a convex posteroventral margin.

The presence of a postorbital ossification appears as a homoplastic character (character 9, Appendix). Although the condition of the postorbital ossification in *Lepturacanthus* and *Trichiurus* (i.e., large, thick, and triangular) is treated as being homologous to that of the other trichiurids possessing a postorbital ossification (i.e., poorly ossified, thin, and irregular in shape), it is possible that the two are not homologous and that the ossification of *Lepturacanthus* and *Trichiurus* represents a unique, derived condition.

Complete loss of the pelvic girdle appears to have occurred only once within the trichiurids. Although absence of the basipterygium (character 39, Appen-

dix) is included in the analysis, five other synapomorphies support the single loss of all pelvic elements at the node uniting *Lepturacanthus* and *Trichiurus* (Fig. 4).

Eupleurogrammus appears as the sister group to *Lepturacanthus* and *Trichiurus*, and the monophyly of these three genera is supported by nine synapomorphies including five homoplasies (Fig. 4). Gill (1863) included *Eupleurogrammus* and *Trichiurus* in the subfamily Lepturinae. His genus *Trichiurus* included *T. savala* Cuvier 1829 (= *Lepturacanthus savala*). Goode and Bean (1895) had already noted the similarity of *Eupleurogrammus* to *Trichiurus* by calling it "a Chinese form" of the latter genus and including both in their own family Trichiuridae. Tucker (1956) excluded *Eupleurogrammus* from the subfamily Lepturinae of Gill (1863). He considered that the presence of a median lateral line, ethmofrontal elevation, pelvic fins, a rounded opercle, and a uniserial row of palatine teeth represents evidence of the close relationship of *Eupleurogrammus* to the lepidopodines and thus its exclusion from the Trichiurinae. My observations differ from those of Tucker (1956) because I found that *Eupleurogrammus* shares with *Lepturacanthus* and *Trichiurus* the presence of a villiform band of teeth covering most of the length of the palatine. Furthermore, the degree of elevation of the frontal ridges on the ethmoidal region appears to be a continuous character among the trichiurid genera *Assurger*, *Evoxymetopon*, *Tentoriceps*, and some species of *Lepidopus*. Although *Eupleurogrammus* is characterized by a frontal bone that is elevated in the ethmoidal region, the condition is different from that present in *Assurger*, *Evoxymetopon*, *Tentoriceps*, and some species of *Lepidopus* (character 23, Appendix). Thus, the original composition of the subfamily Trichiurinae (=Lepturinae of Gill, 1863), including *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*, is supported as a monophyletic group.

Loss of the caudal fin appears to have occurred once within the trichiurids. Monophyly of the four genera that lack a caudal fin (*Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*) is supported by 13 synapomorphies (excluding loss of the caudal fin elements and lack of flexion in the ultimate centrum, characters 56 and 57, respectively, Appendix), of which only two are homoplasies (Fig. 4). However, some authors have questioned the validity of using the presence and absence of a caudal skeleton as a phylogenetically informative character among the trichiurids. Starks (1911) questioned the use of the presence of a caudal fin as a character to define the family Lepidopidae of Goode and Bean (1895), which included *Aphanopus*, *Benthodesmus*, *Evoxymetopon*, and *Lepidopus*. Tucker (1956) placed *Tentoriceps* and *Eupleurogrammus* into two different groups separate from *Lepturacanthus* and *Trichiurus*, which also lack a caudal fin. Further support for the monophyly of

the four ecaudate genera comes from the apparent gradual reduction of the caudal skeleton in *Tentoriceps*, *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*, in that phyletic order. *Tentoriceps* bears some reduced internal elements on the ventral and dorsal margins of the unflexed ultimate centrum. *Eupleurogrammus* bears a well-developed distally expanded haemal spine on the ultimate centrum, whereas *Lepturacanthus* and *Trichiurus* have a thin, pointed haemal spine. Ontogenetic data (Gago, 1997) show that larvae of *Trichiurus* and *Lepturacanthus* bear one or two small cartilaginous plates ventrally at the ultimate centrum. They also have a few short ray-like elements that barely penetrate the skin. This larval condition resembles the reduced caudal skeleton of adult *Tentoriceps*.

Aphanopus appears as the sister group to the rest of the trichiurids (Fig. 4). Parin and Becker (1972) considered *Aphanopus* as the earliest diverging branch within the trichiurids. Tucker (1956) included *Aphanopus*, *Benthodesmus*, and *Diplospinus* within the subfamily Aphanopodinae. Tucker (1956; fig. 23) placed *Aphanopus* as an earlier offshoot of the branch leading to *Benthodesmus*, and *Diplospinus* as a branch that diverges before an apparent trichotomy at the base of his three trichiurid subfamilies.

The subfamilies Aphanopodinae and Lepidopodinae of Tucker (1956) appear as paraphyletic groups in the most parsimonious trees obtained in this study. Tucker's (1956) subfamily Aphanopodinae included *Aphanopus* and *Benthodesmus*, and his subfamily Lepidopodinae included *Assurger*, *Eupleurogrammus*, *Evoxymetopon*, *Lepidopus*, and *Tentoriceps*. In the most parsimonious trees obtained in this study, *Aphanopus*, *Benthodesmus*, *Lepidopus caudatus*-*L. fitchi*, *L. altifrons*-*Evoxymetopon*, *Assurger*, and *Tentoriceps* appear sequentially and in that phyletic order as sister groups to the monophyletic Trichiurinae of Swainson (1839), which includes *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus* (Fig. 4).

No autapomorphies were found that define the genus *Lepidopus* based on the three species available for this study. Some of the data indicate *Lepidopus* to be paraphyletic. All of the three most parsimonious trees obtained separate *L. caudatus* and *L. fitchi* from *L. altifrons*. In these three trees *L. altifrons* appears forming a monophyletic group with *Evoxymetopon* or a trichotomy with *Evoxymetopon* and a clade that includes *Assurger*, *Eupleurogrammus*, *Lepturacanthus*, *Tentoriceps*, and *Trichiurus*.

Three homoplastic characters support node V and the separation of *Lepidopus altifrons* and *Evoxymetopon* from *L. caudatus* and *L. fitchi* (Fig. 4). These three characters are all related to the elevation of the ethmofrontal region (characters 21, 23, and 26; Appendix). No evidence is presented here for the independence of these characters, and it is possible that these three characters are not in-

dependent of each other. Furthermore, as indicated earlier, the degree of elevation of the ethmofrontal region and the convexity of the interorbital space appears to be gradual between *Assurger*, *Eupleurogrammus*, *Evoxymetopon*, *Tentoriceps*, and *Lepidopus*.

Monophyly of the clade *Evoxymetopon-Lepidopus altifrons* is supported in two of the three most parsimonious trees (Fig. 5). However, support for this clade is weak. Only a single character reversal (character 36) supports the monophyly of these two genera. If character 36 is assumed to have evolved independently within the *L. caudatus-L. fitchi* clade (node IVa) and above node V (Fig. 5A), then no support is offered for the monophyly of *Evoxymetopon* and *L. altifrons*.

The first published description of a specimen of *Lepidopus altifrons* is that of Tucker (1957) who identified it as *Evoxymetopon taeniatus*. Parin and Collette (1993; Collette, personal communication) also found that most of the specimens in the USNM and MCZ collections previously identified as *E. taeniatus* were actually specimens of their new species *L. altifrons*.

Parin and Collette (1993) noted that the placement of *Lepidopus altifrons* within the genus *Lepidopus* is arbitrary because it does not fit the diagnostic characters presented by Tucker (1956). Parin (personal communication) has indicated that the species within the genus *Lepidopus* could possibly be separated into different genera. The similarities between *L. altifrons* and *Evoxymetopon* spp. might prove to be evidence in support of such a hypothesis. However, in this study no attempt is made at revising the classification of the genus *Lepidopus*. A revision of the genus *Lepidopus* should await the availability of more specimens of all the *Lepidopus* species for inclusion in an analysis of relationships.

In two of the three most parsimonious trees obtained in this study, *Lepidopus caudatus* and *L. fitchi* appear as a monophyletic group. Support for the monophyly of *L. caudatus-L. fitchi* is based only on the independent acquisition of the derived condition of character 36 (Fig. 5A).

Rosenblatt and Wilson (1987) described the eastern Pacific material previously referred to as *Lepidopus xantusi* as the new species *L. fitchi*. They considered *L. fitchi* not to be conspecific with the original holotype of *L. xantusi* from Cabo San Lucas. They determined that *L. xantusi* represents a synonym of the western Pacific-eastern Atlantic species *L. caudatus*. Such a conclusion places the holotype of *L. xantusi* as the only specimen of *L. caudatus* from the eastern Pacific. Furthermore, their meristic analyses of the number of vertebrae and anal and dorsal-fin rays for the species of *Lepidopus* shows that *L. fitchi* and *L. caudatus* have the lowest and highest ranges for these counts, respectively. The ranges and 95% confidence limits of the means of the meristic counts do not overlap. Even though four other species of *Lepidopus* oc-

cupy an intermediate position between *L. fitchi* and *L. caudatus*, there is no indication of a geographic morphocline. The otoliths of these two species offer more evidence of their morphological differentiation. In addition to the presence of a postcaudal trough, the sagittae of *L. fitchi* have longer, better-defined rostra and antirostra and an overall shape that is different from that of *L. caudatus*. However, this potential character was not included in the analysis because the definition of objective characters states with regard to the degree of extension of the rostrum and antirostrum is difficult.

Parin and Collette (1993) noted that the presence of a convex interorbital space and a sagittal crest that extends onto the ethmoidal region are characters that seem to change in a gradual manner in the series *Lepidopus manis* and *L. fitchi*, *L. caudatus* and *L. calcar*, *L. dubius*, and *L. altifrons*. *Assurger*, *Evoxymetopon*, and *Tentoriceps* could be added to this series as the more derived conditions. In this study, *Tentoriceps* is clearly separated from *Assurger*, *Evoxymetopon*, and *Lepidopus* by 15 synapomorphies that include it in a clade with the other three ecaudate trichiurid genera. *Assurger* is also separated from *Evoxymetopon* and *Lepidopus* and appears as the sister group to the ecaudate trichiurids (Fig. 4, node VI). However, node VI is only supported by a single synapomorphy: the anterior neural spines are distally expanded and forked.

Ontogenetic data (Gago, 1997) have provided evidence that supports several of the arguments of character evolution proposed in this study (Fig. 29). Monophyly of the trichiurids is strongly supported by both the adult and larval data. Furthermore, both data sets also support the monophyly and the same phyletic sequence of the four ecaudate trichiurid genera (*Tentoriceps*, *Eupleurogrammus*, *Lepturacanthus*, and *Trichiurus*). The adult data place *Aphanopus*, *Benthodesmus*, the *Lepidopus fitchi-L. caudatus* clade, the *Lepidopus altifrons-Evoxymetopon* clade, and *Assurger* as the sister groups, in that phyletic sequence, to the ecaudate trichiurids. The larval data (Gago, 1997) also support the position of *Aphanopus* as the most basal trichiurid, but the ontogenetic and adult characters are incompatible with respect to the phyletic placement of *Assurger*, *Benthodesmus*, and *Lepidopus*.

Johnson (1993) noted that specialized larval characters and the patterns of chondrification and ossification in ontogenetic series can be helpful in phylogenetic studies by providing evidence for monophyly and intrarelationships in studies at the family level and below, and by testing hypotheses of homology in adult characters.

In the larval data (Fig. 29), *Assurger* appears as the sister group to the clade that includes *Benthodesmus* and *Lepidopus*. In contrast, in the adult phylogeny (Fig. 4), *Assurger* appears as the sister group of the ecaudate trichiurids, and *Benthodesmus* appears as the sister group to all the trichiurids, except *Aphanopus*. Placement of *Benthodes-*

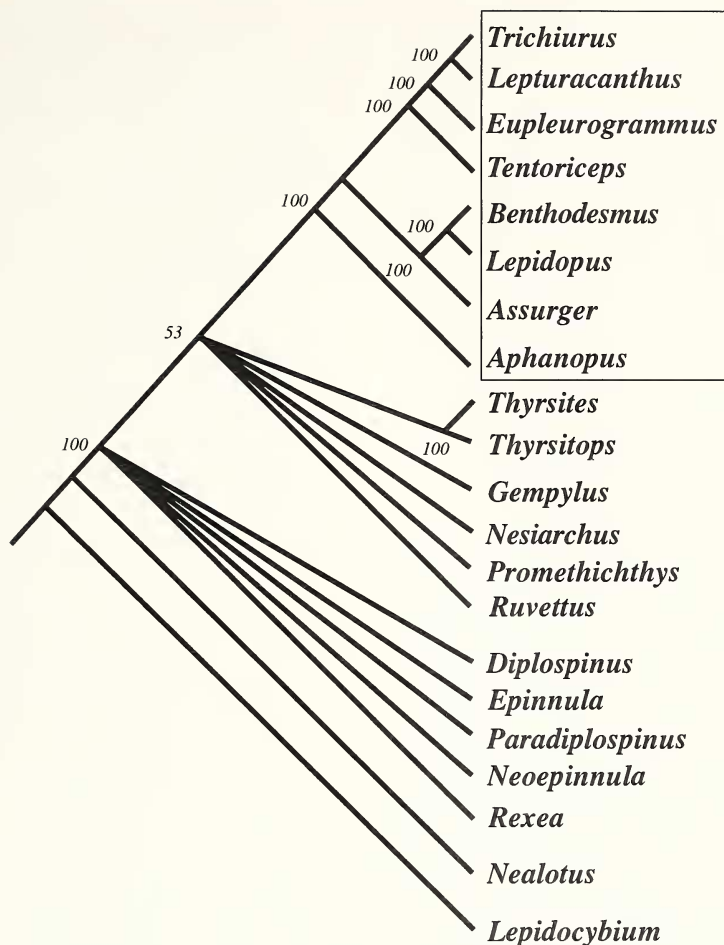


Figure 29. Fifty percent majority rule consensus tree of the 87 equally most parsimonious hypotheses obtained by the branch-and-bound analysis of the larval data of Gago (1997). Numbers indicate the percentage of resulting trees that support those nodes.

mus as the sister group to all trichiurids, except *Aphanopus*, is supported in the adult data matrix by six synapomorphies. In contrast, the monophyly of *Benthodesmus* and *Lepidopus* in the larval phylogeny is only supported by two synapomorphies (i.e., the longitudinal ventral and anterior keels of the pelvic and dorsal spines, respectively, are smooth). Placement of *Assurger* as the sister group to the ecaudate trichiurids in the adult phylogeny (Fig. 4) is supported by one synapomorphy. The sister group relationships of *Assurger* to the clade of *Benthodesmus*-*Lepidopus* in the larval data is also supported by a single synapomorphy (i.e., elongate first dorsal spine). However, the elongation of the first dorsal spine is a subjective character since the degree of elongation among these genera is variable. The larvae of *Lepidopus* have a first dorsal-fin spine that is more than twice the length of the other dorsal-fin spines. In contrast, the first dorsal-fin spine of *Assurger* is only slightly longer

than the other dorsal-fin spines. Furthermore, the condition in *Benthodesmus* has only been reported for the larvae of *B. pacificus* (Ozawa, 1986). Variation in this character is difficult to evaluate because these elongate spines are usually broken during collection.

In the hypothesis of Johnson (1986), the nine genera of cutlassfishes are grouped in the subfamily Trichiurinae within the family Gempylidae, a group that includes the monophyletic Lepidocybiinae and the apparently paraphyletic Gempylinae. Johnson (1986) considered his Trichiurinae as a highly derived branch of the gempylids. Although I also consider the trichiurids as being closely related to the gempylids, the development of a formal classification for the cutlassfishes, at this point in time, is unwarranted. I agree with Carpenter et al. (1995) that a formal classification for the gempylids and trichiurids (superfamily Trichiuroidea) must await a combined analysis of both groups.

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APPENDIX

List of Characters

Characters are grouped together according to structural units or types (e.g., neurocranium). The numbers refer to the character number as shown in Table 1. Character states are within parentheses.

OPERCULAR SERIES

1. Posterior and ventral margins of opercle, subopercle, and interopercle. Complete; only the dorsal flap of the opercle and the posterior corner of the subopercle may be slightly splintered (0). Strongly splintered or fimbriate (1).
2. Lateral process on articular head of the opercle. Plate-like and covering most of the articular fossa of the bone (0). Elongate and flat in cross section (1). Elongate and round in cross section (2).
3. Fimbriations on posteroventral corner of the subopercle. Not much longer than the preceding ventral ones, giving a convex appearance to the ventral margin of the bone (0). Much more elongate than the preceding ventral ones, giving a slightly concave appearance to the ventral margin of the bone (1).
4. Articular process of subopercle. Extends dorsally at a right angle, articulating mainly with the anteroventral corner of the opercle (0). Extends anteriorly and articulates mainly with the posterodorsal corner of the interopercle (1).
5. Posterodorsal margin of preopercle. Convex (0). Concave (1).

CIRCUMORBITAL SERIES

6. Circumorbital series. Complete (0). Incomplete with a short gap between the first infraorbital elements and

the postorbitals (1). Extremely reduced; only the lachrymal and jugal are present (2).

7. Shape of ventral wing of lachrymal. Ovoid; fimbriations in the anterior and posterior margins of the ventral wing are not perpendicular to the dorsal, longitudinal, lateral-line canal (0). Quadrilateral; fimbriations in the anterior and posterior margins of the ventral wing are nearly perpendicular to the dorsal, longitudinal, lateral-line canal (1).
8. Posterodorsal plate of lachrymal. Short; ends before or above the posterior pore of the longitudinal, dorsal lateral-line canal (0). Elongate; extends past the posterior pore of the longitudinal, dorsal lateral-line canal ending above the jugal (1).
9. Postorbital ossification. Absent (0). Reduced and thin (1). Large and thick (2).

JAWS

10. Dentary and premaxillary fangs and serial teeth. Smooth (0). Serrate (1).

SUSPENSORIUM

11. Posterodorsal process of quadrate. Long; extends well past the ventral margin of the metapterygoid (0). Short; does not extend well past the ventral margin of the metapterygoid (1).
12. Posteromedial arm of ectopterygoid. Does not reach the metapterygoid (0). Reaches the metapterygoid (1).
13. Well-developed condyle posterior to anteromedial

shelf of palatine. Absent (0). Present and visible in lateral view (1).

14. Teeth on ventral margin of palatine. Large and few; a single row covering only a very small portion of the ventral margin of the bone (0). Small and numerous; in several rows covering most of the ventral margin of the bone (1).

HYOID COMPLEX

15. Anterodorsal corner of ceratohyal. Not pointed; does not extend anteriorly (0). Pointed; extends anteriorly abutting the dorsal margin of the dorsal hypohyal (1).
16. Shape of posteroventral processes of glossohyal in ventral view. Neither triangular nor quadrilateral; do not have their lateral corners pointing posteriorly (0). Wing-like, with corners pointed posteriorly (1). Quadrilateral (2). Triangular (3).

BRANCHIAL COMPLEX

17. Shape of articular head of first basibranchial. Tapers to a point; not knob-like (0). Knob-like, but not bearing dorsolateral processes (1). Knob-like and bearing dorsolateral processes (2).
18. Laterally pointed processes on second basibranchial. Absent (0). Present (1).
19. Shape of fourth ceratobranchial. Straight (0). Sigmoidal (1).

NEUROCRANIUM

Ethmoidal Region

20. Anterior tip of nasal. Straight (0). Curved; giving the bone a concave lateral margin in dorsal view (1).
21. Dorsal ridges on ethmoid. Absent or reduced; do not extend well above the nasals in lateral view (0). Present; extend well above the nasals in lateral view (1).
22. Connection of supraorbital and infraorbital lateral-line canals. Supraorbital lateral-line canal connects with the infraorbital canal through a dorsally or laterally directed pore (0). Lateral bony tubular extension of supraorbital lateral-line canal to orbital rim (1).
23. Elevation of frontal ridges on ethmoidal region. Not elevated (0). Elevated; laterally convex (1). Extremely elevated; appear as laterally flat sheets (2).

Orbital Region

24. Sclerotics. Present (0). Absent (1).

Otic Region

25. Supraoccipital crest. Reduced; runs close to and parallel to the epiotic ridges; dorsal profile of the neurocranium is flat in lateral view (0). Dorsally expanded; runs higher and not parallel to the epiotic ridges; dorsal profile of the neurocranium is not flat in lateral view (1).
26. Highest point of supraoccipital crest. Posterior to the orbits (0). Above the orbits (1).
27. Pterotic. Ends before the posterior margin of the neurocranium (0). Ends well past the posterior margin of the neurocranium (1).
28. Intercalar. Visible dorsally (0). Not visible dorsally (1).
29. Exoccipital ridge. Reaches the vagus foramen (0). Does not reach the vagus foramen (1).

PECTORAL GIRDLE

30. Length of dorsal articular process of posttemporal. Short; ends before or slightly past the anterior margin of the supratemporal (0). More than twice the length of the supratemporal (1).
31. Posteroventral process of posttemporal. Absent (0). Reduced, flat in cross section; comes in contact or close association with the articular head of the supracleithrum (1). Long, round in cross section; does not come in contact or close association with the articular head of the supracleithrum (2).
32. Anteroventral process of posttemporal. Originates on the posterior corner of the bone (0). Shares a common origin with the posteroventral process; close to or on the anterior half of the canal-bearing portion of the bone (1). Separate from the posteroventral process; originates close to or on the anterior half of the canal-bearing portion of the bone (2).
33. Posterodorsal corner of posttemporal. Not expanded (0). Expanded (1).
34. Articular head of the supracleithrum. Posteriorly expanded; bears a completely enclosed canal that transmits the lateral line to the posttemporal (0). Posteriorly expanded; bears an open canal or shelf connecting the lateral line to the posttemporal (1). Not expanded; lacks a canal (2).
35. Lateral process on articular head of supracleithrum. Absent (0). Present (1).
36. Anteroventral process on articular head of supracleithrum. Absent (0). Present (1).
37. Posteroventral plate on coracoid. Absent; ventral margin of coracoid is flat; its posterior corner ending before the fourth radial (0). Present; ventral margin is round; its posterior corner ending past the fourth radial (1).
38. Length of pectoral-fin rays. Posterior fin rays are longer (0). Anterior fin rays are longer (1).

PELVIC GIRDLE

39. Basipterygium. Present (0). Absent (1).
40. External spinous elements of pelvic fin. Spine-like (0). Scale-like (1).
41. Position of basipterygium. Thoracic; articular facet is anterior to distal tip of ventral postcleithrum (0). Abdominal; articular facet is posterior to distal tip of ventral postcleithrum (1).
42. Central part of basipterygium. Dorsally inclined (0). Nearly parallel to the ventral body wall (1).
43. Central part of basipterygium. Bilaterally divided (0). Longitudinally fused (1).

AXIAL SKELETON

Vertebral Column

44. Total number of vertebrae. 30–55 (0). 57–67 (1). 84–198 (2).
 45. First neural spine. Not distally bifurcate (0). Distally bifurcate (1).
 46. Anterior neural spines. Not expanded or forked distally (0). Expanded and forked distally (1).
- Intermusculars
47. Series of unattached epineurals and epicentrals extending into caudal region. Both present (0). Only the epineural series present (1). Both absent (2).

Dorsal and Anal Fins

48. Notch in the fin membrane separating the spinous and soft portions of the dorsal fin. Present (0). Absent (1).
49. Spinous portion of the dorsal fin. XIX–XXXIX spines; its base is longer than that of the soft portion (0). XXXVIII–XLV spines; its length is only slightly shorter than length of soft portion (1). XXXI–XLVI spines; its base is less than half of the length of the soft portion but not extremely short (2). Only III–X spines; its base is extremely short compared to the base of the soft portion (3).
50. Number of radials in soft dorsal-fin pterygiophores. 2; proximal-middle and distal (0). 3; proximal, middle, and distal (1).
51. Proximal-middle radial of first dorsal pterygiophore. Does not extend above occiput (0). Extends above occiput (1).
52. Foramen at anteroventral corner between the proximal and distal portions of the dorsal-fin proximal radials. Absent (0). Present (1).
53. Number of supernumerary elements on first anal-fin pterygiophore. Two (0). One (1).
54. Anal-fin soft rays. Well-developed soft rays throughout the whole length of the anal fin (0). Well-developed soft rays only in the posterior portion of the anal fin (1). Modified as small spinule-like elements (2). Reduced to small scale-like ossifications that do not penetrate the epithelium (3). Modified into small fused knobs that barely penetrate the epithelium (4).
55. Anal-fin pterygiophores. Two (proximal-middle and

distal) or three (proximal, middle, and distal) radials present (0). The proximal, middle, and distal radials are fused with each other and appear as a single unit (1).

CAUDAL COMPLEX

56. Caudal complex. Well developed (0). Reduced to a few small internal elements (1). Absent (2).
57. Ultimate centrum. Flexed and forming a urostyle (0). Not flexed (1).
58. Number of epurals. Three (0). Two (1). One (2).
59. Haemal and neural spines of preural centrum 4. Long; extends past or as far as the posterior margin of the preural centrum 3 (0). Short; does not extend well past the anterior margin of the preural centrum 3 (1).
60. Hypural plates formula. I + II + III + IV + V (0). I–II + III–IV + V (1). I–II + III–IV–V (2).
61. Hypural notch. Large (0). Small (1).
62. CMC cartilage. Absent (0). Present (1).
63. CPNPU3 cartilage. Present (0). Absent (1).

OTOLITHS

64. Excisura. Delimited by a well-developed rostrum and antirostrum (0). Delimited by a reduced rostrum and antirostrum (1).
65. Cristae superior and inferior. Reduced (0). Well developed and overhanging (1).
66. Longitudinal ridge on the ostium. Absent (0). Present (1).